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All the abbreviations and acronyms used in the text should be explained, preferentially under Material and methods. Use the standard abbreviations for measure units (e.g. "m", not "mt." for metre) and the official institutional acronyms.
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Example of systematic hierarchy and synonymy:
Family Cardiidae Lamarck, 1809
Subfamily Cardiinae Lamarck, 1809
Genus *Acanthocardia* Gray, 1853
(type species *Cardium aculeatum* Linné, 1758)

Cardium indicum Lamarck, 1819
(Fig. 1. A-D, Fig. 2. C)

Cardium hians Brocchi, 1814: p. 508, pl. 13, fig. 6 (non Spengler, 1799).
Cardium indicum Lamarck, 1819: p. 4.
Cardium (Cardium) indicum Lamarck - Fischer-Piette, 1977: p. 112, pl. 10, fig. 4 (type).

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Example of citations:
... reported by Richardson & Smith (1965)
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Example of references:
Salas C., 1996. Marine Bivalves from off the Southern Iberian Peninsula collected by the Balgim and Fauna 1 expeditions. *Haliotis*, **25**: 33-100.
Grill B. & Zuschin M., 2001. Modern shallow- to deep-water bivalve death assemblages in the Red Sea - ecology and biogeography. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **168**: 75-96.
Boss K.J., 1982. Mollusca, in Parker S.P. (ed.), *Synopsis and Classification of Living Organisms*. Vol. 1. McGrow-Hill, New York: 945-1166.
Carter J.G., Campbell D.C. & Campbell M.R. 2000. Cladistic perspectives on early bivalve evolution, in Harper E.M., Taylor J.D. & Crame J.A. (eds), The Evolutionary Biology of the Bivalvia. *Geological Society, London, Special Publications*, **177**: 47-95.
Vokes H.E., 1980. *Genera of the Bivalvia: a systematic and bibliographic catalogue (revised and update)*. Paleontological Research Institution, Ithaca, Edwards Brothers Inc., 307 pp.

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Boll. Malacol., **55**: 105-106 (2, 30/11/2019)

Spinochitonidae fam. nov. and Spinochiton gen. nov. (Mollusca: Polyplacophora) redefined to meet the requirements of the Article 8.5 of the ICZN

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Abstract

The name *Spinochiton* gen. nov. (and in turn Spinochitonidae fam. nov.), published by Dell'Angelo et al. (2018) is invalid due to it being based on the type species *Chaetopleura gaasi* Cherns & Schwabe, a name that was not yet available at the time of publication of *Spinochiton* gen. nov. This problem arose because the trivial name that appeared online in an"early view" version of *Historical Biology* does not meet the requirements of the ICZN for electronic publications. The two names *Spinochiton* gen. nov. and Spinochitonidae fam. nov. are herein made available.

Key Words

Mollusca, Polyplacophora, Systematics, taxonomic redefinition

Riassunto

Spinochiton gen. nov. (ed a sua volta Spinochitonidae fam. nov.), pubblicato da Dell'Angelo et al. (2018), non è valido in quanto basato sulla specie tipo *Chaetopleura gaasi* Cherns & Schwabe, un taxon che non era ancora disponibile al momento della pubblicazione di *Spinochiton* gen. nov. Il problema è causato dal fatto che il nome apparso sulla versione online di *Historical Biology* non soddisfaceva i requisiti di ICZN per la pubblicazione elettronica. *Spinochiton* gen. nov. e Spinochitonidae fam. nov. vengono pertanto ridefiniti e resi disponibili.

Parole chiave

Mollusca, Polyplacophora, Sistematica, ridefinizione tassonomica

Introduction

Cherns & Schwabe published online (01 Nov 2017) in "*Historical Biology*" a paper on Eocene and Oligocene chitons from the Paris and Hampshire Basins, with the description of five new species. One of these was *Chaetopleura gaasi*, a description based on four valves (three head and one tail) from the Oligocene (Rupelian) of Gaas (Aquitaine, France). The paper has been published in print version in Volume 31, 2019 – issue 6 of *Historical Biology*.

Dell'Angelo et al. (2018) published in "*Bollettino Malacologico*" (30 June 2018) the first part of a paper on Oligocene to Miocene chitons of the Aquitaine and Ligerian Basins (France), including material from Gaas, and the same species described by Cherns & Schwabe as *Chaetopleura gaasi*. This work was completed in April 2017 and sent to the Editor of "*Bollettino Malacologico*" as early as May 8th, and for the species described by Cherns & Schwabe as *Chaetopleura gaasi* a new family (Spinochitonidae), a new genus (*Spinochiton*) and a new species were erected.

The work of Cherns and Schwabe has been released electronically (01 Nov 2017) while our ms was under review, and therefore, we decided to remove the description of the 'new species', maintaining the introduction of the new genus *Spinochiton* and the new family Spinochitonidae, and changed the generic assignment of *Chaetopleura gaasi* from *Chaetopleura* to *Spinochiton*, as type species.

However, Philippe Bouchet (Muséum National d'Histoire Naturelle) pointed out to us that the name *Chaetopleura gaasi* is not yet an available name. The "early view" version of the *Historical Biology* paper does not meet the requirements of the ICZN for electronic publications (ICZN, 1999: Art. 8.5, no ZooBank registration) and therefore, the paper was nomenclaturally available publication only from the print version of the journal. Thus, *Chaetopleura gaasi* was still an unavailable name on June 30th, 2018 – and thus the names *Spinochiton* and Spinochitonidae are also unavailable because they were not based on an available type species / type genus.

Discussion

The two names Spinochitonidae fam. nov. and *Spinochiton* gen. nov. must therefore be redefined after the availability of the print version of Cherns & Schwabe's paper in Volume 31, 2019 – issue 6 of *Historical Biology*.

Family Spinochitonidae new family

Type genus

Spinochiton new genus.

Diagnosis

See Dell'Angelo et al. (2018: p. 34).

Occurrence

Known only from the middle Oligocene (Rupelian) of Gaas, Aquitaine Basin (France).

Remarks

See Dell'Angelo et al. (2018: p. 34).

Genus *Spinochiton* new genus

Type species

Spinochiton gaasi (Cherns & Schwabe, 2019).

Diagnosis

As for new family.

Occurrence

Known only from the Middle Oligocene (Rupelian) of Gaas, Aquitaine Basin (France).

Etymology

The name refers to the sculpture of radial rows of conical spinous processes.

Remarks

See Dell'Angelo et al. (2018: p. 34).

Acknowledgements

The authors wish to thank Philippe Bouchet (Muséum National d'Histoire Naturelle, Paris, France) for kindly addressing to us the nomenclatural complications discussed herein, and Marco Oliverio (Department of Biology and Biotechnologies "Charles Darwin", Sapienza University of Rome, Italy) and Bernard M. Landau (Naturalis Biodiversity Center, Leiden, The Netherlands) for the useful comments.

References

Cherns L. & Schwabe E., 2019. Eocene and Oligocene chitons (Polyplacophora) from the Paris and Hampshire Basins. *Historical Biology*, **31** *(6): 684-695*. DOI: 10.1080/08912963.2017.1387545 (published online 01 Nov 2017).

Dell'Angelo B., Lesport J.F., Cluzaud A. & Sosso M., 2018. The Oligocene to Miocene chitons (Mollusca: Polyplacophora) of the Aquitaine Basin, southwestern France, and Ligerian Basin, western France. Part 1: Leptochitonidae, Hanleyidae, Ischnochitonidae, Chitonidae, Spinochitonidae fam. nov. and Schizochitonidae. *Bollettino Malacologico*, **54** (1): 1-47 (published 30 June 2018)

ICZN [International Commission on the Zoological Nomenclature], 1999. *International Code of the Zoological Nomenclature, Fourth Edition, Adopted by the International Union of Biological Science*, International Trust for the Zoological Nomenclature, Padova, xxix + 306 pp.

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The original descriptions of the Mediterranean taxa in the order Myopsida (Mollusca: Cephalopoda)

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Abstract

The original descriptions of the Mediterranean taxa in the order Myopsida d'Orbigny, 1841 are reported and discussed. The correct scientific name, authorship and publication date for these taxa are also established. The seven taxa included in the present work are: family Loliginidae Lesueur, 1821; genus *Loligo* Lamarck, 1798 and its species *Loligo vulgaris* Lamarck, 1798 and *Loligo forbesii* Steenstrup, 1856; genus *Alloteuthis* Wülker, 1920 and its species *Alloteuthis media* (Linnaeus, 1758) and *Alloteuthis subulata* (Lamarck, 1798). The exact reference for the paper containing the names *Loligo, L. vulgaris* and *A. subulata* was established.

Key words

Cephalopoda, Myopsida, Mediterranean Sea, nomenclature, *Alloteuthis*.

Riassunto

[*Le descrizioni originali dei taxa mediterranei dell'ordine Myopsida (Mollusca: Cephalopoda)*]. In questo lavoro sono riportate e discusse le descrizioni originali dei taxa nell'ordine Myopsida d'Orbigny, 1841, e, di questi, viene definita l'esatta nomenclatura completa di paternità, data di pubblicazione e referenza bibliografica. Sono, inoltre, riferite varie informazioni relative alle suddette descrizioni originali. I taxa trattati sono: famiglia Loliginidae Lesueur, 1821, genere *Loligo* Lamarck, 1798 con le specie *Loligo vulgaris* Lamarck, 1798 e *Loligo forbesii* Steenstrup, 1856; genere *Alloteuthis* Wülker, 1920 con le specie *Alloteuthis media* (Linnaeus, 1758) e *Alloteuthis subulata* (Lamarck, 1798). In particolare, viene definita l'esatta referenza bibliografica relativa ai nomi *Loligo, L. vulgaris* e *A. subulata*.

Parole chiave

Cephalopoda, Myopsida, Mediterranean Sea, nomenclature, *Alloteuthis*.

Introduction

Following two papers on the original descriptions of the Mediterranean cephalopod taxa in the orders Sepiida Zittel, 1895 (including Spirulidae Rafinesque, 1815) (Bello, 1996) and Sepiolida Fioroni, 1981 (Bello, 2015), the present one deals with the group Myopsida d'Orbigny, 1841.

This paper is in line with the previous papers as for its genesis and purpose. Thus, it aims at establishing, by means of the original documents and in agreement with the International Code of Zoological Nomenclature (ICZN, 1999), the correct scientific names with proper authorship and publication date to be used in taxonomic works. Only the taxonomic levels taken into consideration by the ICZN (1999) are dealt with here, namely family, genus and species ranks.

The traditional subdivision of the order Teuthida Naef, 1916 into the suborders Myopsida and Oegopsida d'Orbigny, 1841 (e.g. Sweeney, 2001), has been recently challenged by molecular analyses, according to which Myopsida and Oegopsida are not sister taxa (Allcock et al., 2014). Accordingly, Myopsida will be here considered an order, subdivided into the families Australiteuthidae Lu, 2005 and Loliginidae Lesueur, 1821 (Vecchione & Young, 2016). Only the latter family is represented in the Mediterranean Sea by five species belonging to three different genera. Among these species, one is a comparatively recent Lessepsian migrant, which established a viable population in this basin, assigned to *Sepioteuthis lessoniana* Férussac in Lesson, 1830 by Salman & Katagan (2002) and subsequent workers (e.g. Lefkaditou et al., 2009). Indeed, this nominal species is deemed a cryptic species complex, encompassing several specific entities (e.g. Segawa et al., 1993); moreover, Okutani (2015) ascribed the Red Sea population (that is the population from which some individuals migrated into the Mediterranean) to *Sepioteuthis loliginiformis* (Rüppell & Leuckart, 1828). These facts indicate that the specimens caught in the Mediterranean will be probably assigned to a species other than *S. lessoniana* in the next future. Hence, I shall not deal with this nominal taxon here in order not to endorse it and shall postpone its treatment until the taxonomic position of those Mediterranean specimens will be solved.

In all, seven taxa are dealt with and discussed.

Materials and Methods

The present paper is based on the examination of the actual documents reporting the original descriptions of the Mediterranean taxa in the order Myopsida, as well as other papers, including Sweeney (2001), which was the reference base. The bibliographic search was carried out in the library of several scientific institutions, mainly the Stazione Zoologica in Naples (Italy) and the Muséum National d'Histoire Naturelle in Paris.

The term 'description' *sensu lato* embraces also the 'definition' and the 'diagnosis' (cf. the Glossary in the ICZN, 1999).

Each taxon entry includes the valid name complete of its author and publication date; full reference to the work containing the original description, followed, in square brackets [], by the language used; original spelling (and combination, for specific names); corrected name, where necessary; description (specifically, whether description, definition, diagnosis or indication) in the original language and its English translation, as literally as possible, in braces { }; derivation of generic and specific names; type locality of species; type repository of species; name-bearing type; list of genera and species originally included in the family and genus, respectively; notes, comments, and additional information, under the heading Remarks. The use of the original typographical characters was retained, as far as possible, in reporting quotations.

As for the Danish writings by Steenstrup on *Loligo forbesii*, a new, direct translation was provided, since the available English version (Steenstrup, 1857b) was not fully satisfactory.

Only in two cases I pointed out, by a [sic!] in square brackets, printing mistakes or other types of inaccuracies concerning the linguistic domain. Also my interpolations are reported in square brackets [...]. Within each family and genus, genera and species are respectively listed in chronological order.

Original dscriptions

Family Loliginidae Lesueur, 1821

Original spelling: Loligoidea (p. 89).

Corrected name

Loliginidae. From the stem of *loligo* in the genitive singular case *loligin-is* → Loligin-idae (ICZN: art. 29.3.1), instead of the original formation Loligo-idea.

Work

C.A. Lesueur, 1821. Descriptions of several new species of Cuttle-fish. *Journal of the Academy of Natural Sciences of Philadelphia*, 2(1): 86-101. [In English]

Definition (p. 89)

"Characters.--Body enclosed in a sac, which is elongated, narrow, cylindrical, subulate posteriorly; fins terminal, united or separate; bone very thin, more or less transparent, sometimes partially gelatinous; arms as in the Sepia, with or without long arms."

Type genus

Loligo.

Other genera originally included in the family

Leachia and *Onykia*.

Remarks

Lesueur (1821) criticized, in very soft tones, Leach's (1817) decision to subdive the order Decapoda into only two families, i.e. Sepiolidea [= Sepiolidae Leach, 1817] and Sepiidea [= Sepiidae Leach, 1817], the latter containing *Sepia* Linnaeus, 1758 and *Loligo* (cf. Bello, 1996 and 2015). Leueur (loc. cit.) pointed out the oddity of that subdivision and the resulting need to create a new family to contain the decapod species with a non-calcareous 'bone' and a cylindrical body with terminal fins, which distinguishes them from *Sepiola*.

Some of the genera and species originally included in Loliginidae by Lesueur (1821) are presently distributed in families other than Loliginidae: *Leachia* and *Loligo* [= *Taonius*] *pavo* in Cranchiidae Prosch, 1847, *Loligo* [= *Ommastrephes*] *bartramii* and *Loligo* [= *Illex*] *illecebrosa* in Ommastrephidae Steenstrup, 1857, *Onykia* and *Loligo bartlingii* [a synonym of *Onychoteuthis banksii* (Leach, 1817)] in Onychoteuthidae Gray, 1849 (cf. Sweeney, 2001). In fact, Loliginidae as meant by its Author (Lesueur, 1821) approximately correspond to the present taxa Myopsida + Teuthida.

As a side issue, it is noteworthy that Lesueur (1821) dedicated his new genus *Leachia* to the Author whose work he had criticized (see above): a fine example of savoir faire in zoological science.

Genus *Loligo* Lamarck, 1798

Original spelling

Loligo (p. 130).

Work

[J.-B.] Lamarck, 1798. *Extrait d'un Mémoire sur le genre de la* Sèche, *du* Calmar *et du* Poulpe, *vulgairement nommés*, Polypes de mer. *Bulletin des Sciences, par la Société Philomatique de Paris*, 1(17): 129-131. [In French; species definitions in Latin]

Definition (genus II)

"Calmar. *Loligo*.

Caractère. Corps charnu, allongé, contenu dans un sac ailé inférieurement, et renfermant vers le dos un corps mince, transparent, corné.
Bouche terminale, entourée de dix bras qui couronnent la tête, sont garnis de ventouse verruciformes, et dont deux sont plus longs que les autres." (p. 130)
{*Character.* Body fleshy, lengthened, enclosed in a sac inferiorly [indeed, posteriorly] winged, and dorsally containing a thin, transparent, horny object [i.e. the gladius]. Mouth terminal, surrounded by ten arms encircling the head, provided with verruca-like suckers, two of which are longer than the others.}

Derivation of name

Not stated. From *lolligo* (Latin), squid.

Gender

Feminine.

Type species

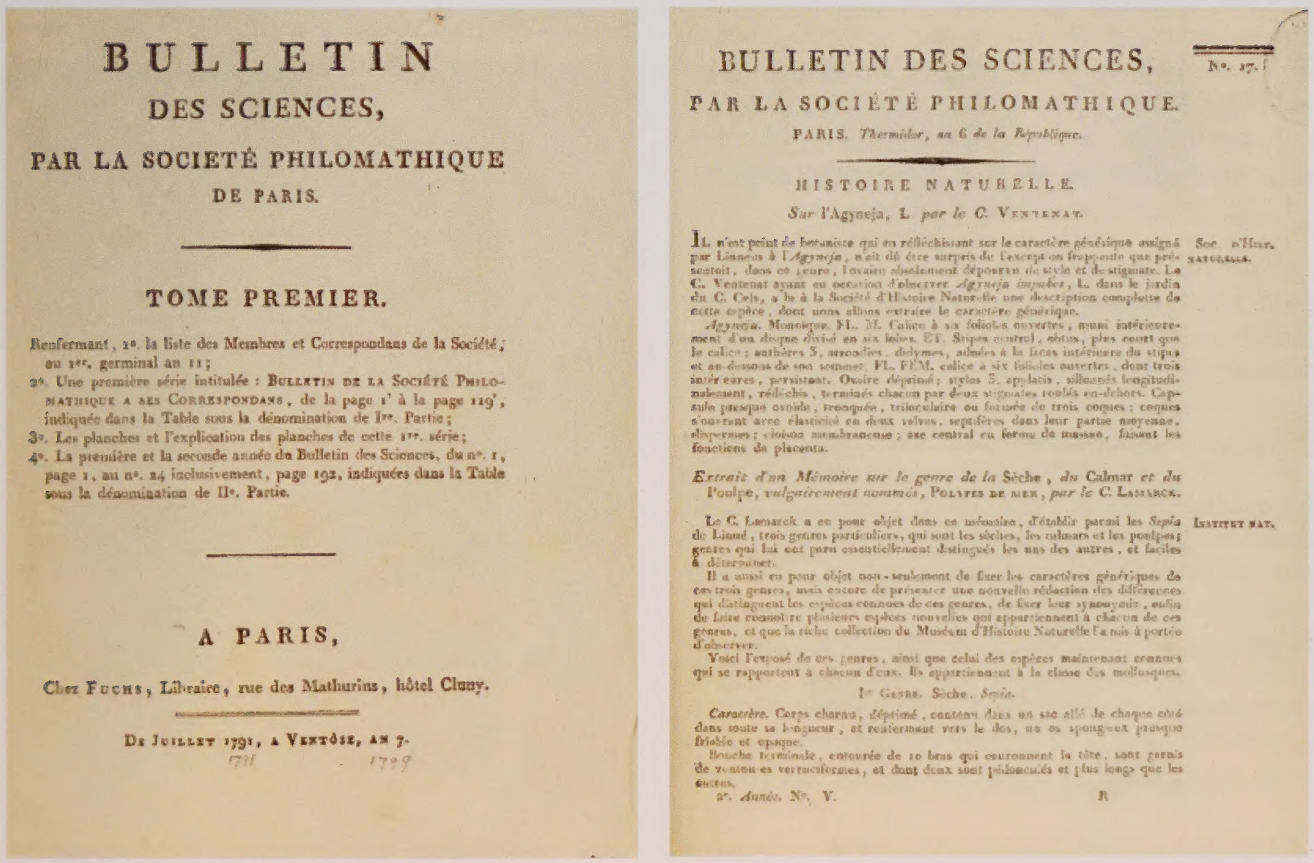
Loligo vulgaris Lamarck, 1798, by subsequent designation by Children (1824).

Species originally included in the genus

L. vulgaris, L. sagittata [= *Todarodes sagittatus*] (cf. Sweeney, 2001), *L.* [= *Alloteuthis*] *subulata* and *L. sepiola* [= *Sepiola rondeletii* Leach, 1817 with implied reference to Linnaeus (1758); under this specific name all Sepiolinae species were lumped (Bello, 2015)].

Remarks

Lamarck subdivided the known living cephalopods into three genera, namely *Sepia, Loligo* n.g. and *Octopus*. Accordingly, his description of *Loligo*, which in fact includes today's Sepiolidae, is sufficient to discriminate its members from cuttlefishes and octopuses. Incidentally, the English collective name 'squid' coincides with the genus *Loligo* as meant by Lamarck. The paragraph "*Observation*", a sort of diagnosis, further compares *Loligo* with the other two genera and corroborates it.
The paper by Lamarck (1798) was based on specimens in the Muséum d'Histoire Naturelle in Paris. As for the bibliographic reference for the original description of this genus, the right volume and issue indication is vol. 1 issue 17, rather than vol. 2 issue 5 as given in recent repertoires (e.g. MolluscaBase, 2019). In fact, the 1st volume of the *Bulletin des Sciences* published by the *Société Philomatique de Paris* spanned from "Juillet 1791" to "Ventóse, an 7" (Fig. 1) – the latter date in terms of the French Republican Calendar – which month ended on the 20th March 1799. Lamarck's paper was published in the month of "Thermidor, an 6 de la République" (19th of July – 17th of August 1798) (**Fig. 1**). When citing this



BULLETIN
DES SCIENCES,
PAR LA SOCIETÉ PHILOMATHIQUE
DE PARIS.

TOME PREMIER.

Renfermant, 1°. la liste des Membres et Correspondans de la Société; au 1er. germinal an 11;
2°. Une première série intitulée : Bulletin de la Société Philomathique a ses Correspondans, de la page 1' à la page 119', indiquée dans la Table sous la dénomination de Ire. Partie;
3°. Les planches et l'explication des planches de cette 1re. série;
4°. La première et la seconde année du Bulletin des Sciences, du n°. 1, page 1, au n°. 24 inclusivement, page 192, indiquées dans la Table sous la dénomination de IIe. Partie.

A PARIS,

Chez Fuchs, Libraire, rue des Mathurins, hôtel Cluny.

De Juillet 1791, a Ventôse, an 7.

BULLETIN DES SCIENCES, N°. 17.
PAR LA SOCIÉTÉ PHILOMATHIQUE.
PARIS. *Thermidor, an 6 de la République.*

HISTOIRE NATURELLE.

Sur l'Agneja, L *par le* C. Ventenat.

Il n'est point de botaniste qui en réfléchissant sur le caractère générique assigné par Linnæus à l'*Agneja*, n'ait dû être surpris de l'exception frappante que présentoit, dans ce genre, l'ovaire absolument dépourvu de style et de stigmate. Le C. Ventenat ayant eu occasion d'observer *Agneja impudica*, L. dans le jardin du C. Cels, a lu à la Société d'Histoire Naturelle une description complette de cette espèce, dont nous allons extraire le caractère générique.

Agneja. Monoïque. Fl. M. Calice à six folioles ouvertes, aussi intérieurement d'un duvet divisé en six loges. Et. Stipes central, épais, plus court que le calice; anthères 5, arrondies, didymes, adnées à la face intérieure du stipes et au-dessous de son sommet. Fl. FEM. calice à six folioles ouvertes, dont trois intérieures, persistant. Ovaire dépourvu; styles 5, applatis, silloneés longitudinalement, réfléchis, terminés chacun par deux stigmates roulés en-dehors. Capsule presque ovoïde, trouquée, triloculaire ou formée de trois coques; coques s'ouvrant avec élasticité en deux valves, septifères dans leur partie moyenne, éspermes; cloison membraneuse; axe central en forme de massue, faisant les fonctions de placenta.

Extrait d'un Mémoire sur le genre de la Sèche, *du* Calmar *et du* Poulpe, *vulgairement nommés*, Polypes de mer, *par le* C. Lamarck.

Le C. Lamarck a eu pour objet dans ce mémoire, d'établir parmi les *Sepia* de Linné, trois genres particuliers, qui sont les sèches, les calmars et les poulpes; genres qui lui ont paru essentiellement distingués les uns des autres, et faciles à déterminer.

Il a aussi eu pour objet non-seulement de fixer les caractères génériques de ces trois genres, mais encore de présenter une nouvelle rédaction des différences qui distinguent les espèces connues de ces genres, de fixer leur synonymie, enfin de faire connoître plusieurs espèces nouvelles qui appartiennent à chacun de ces genres, et que la riche collection du Muséum d'Histoire Naturelle l'a mis à portée d'observer.

Voici l'exposé de ces genres, ainsi que celui des espèces maintenant connues qui se rapportent à chacun d'eux. Ils appartiennent à la classe des mollusques.

Ier Genre. Sèche. *Sepia.*

Caractère. Corps charnu, déprimé, contenu dans un sac ailé de chaque côté dans toute sa longueur, et renfermant vers le dos, un os spongieux presque friable et opaque.

Bouche terminale, entourée de 10 bras qui couronnent la tête, sont garnis de ventouses verruciformes, et dont deux sont pédonculés et plus longs que les autres.

2e. *année.* N°. V. R

Soc. d'Hist. naturelle.

Institut nat.

Fig. 1. Opening page of the 1st volume of the *Bulletin des Sciences, par la Société Philomatique de Paris* (left) and opening page of the 17th issue of the same volume (right).

Fig. 1. Pagina d'apertura del 1° volume del *Bulletin des Sciences, par la Société Philomatique de Paris* (a sinistra) e pagina d'apertura del 17° numero dello stesso volume (a destra).

reference, it is necessary to give also the issue number, i.e. 17, since the page foliation is not continuous throughout the issues.
As a further consequence of the French Revolution (1789), a "C.", abbreviation of Citoyen [= Citizen] was put before Lamarck's surname and both the whole set of given names and, obviously, the nobiliary prepositive 'de' omitted. The full name of the great French scientist was Jean-Baptiste-Pierre-Antoine de Monet chevalier de Lamarck (**Fig. 2**).
Loligo Lamarck, 1798 is placed on the *Official List of Generic Names in Zoology* (Anonymous, 2012). The name *loligo* was used by Linnaeus (1758) as a specific epithet and was therefore suppressed under the plenary power of the International Commission for Zoological Nomenclature (Op. 1861) for the purposes of the Principle of Priority but not for those of the Principle of Homonymy (Anonymous, 2012). The name *Loligo* Schneider, 1784 was deemed a cheironym (unpublished name) and hence not made available (Hemming, 1954).

Species *Loligo vulgaris* Lamarck, 1798

Original spelling and combination

Loligo vulgaris (p. 130).

Work

[J.-B.] Lamarck, 1798. *Extrait d'un Mémoire sur le genre de la* Sèche, *du* Calmar *et du* Poulpe, *vulgairement nommés,* Polypes de mer. *Bulletin des Sciences, par la Société Philomatique de Paris.* 1(17): 129-131. [In French; specific definitions in Latin]

Definition (species no. 1 of the genus *Loligo*, "1. Calmar commun. *Loligo vulgaris*")

"Loligo alis semi-rhombeis [sic! for rhombicis], limbo sacci trilobo, lamina dorsali antice angustata." (p. 130) {Loligo with wings [= fins] semi-rhombic, sac border trilobate, dorsal lamina [= gladius] anteriorly narrow.}

Derivation of name

Not stated. From *vulgaris* (Latin; feminine: *vulgaris*), common. The Latin name corresponds to the French one and refers to its abundance in catches.

Type locality

Not stated.

Type repository

"Muséum d'Histoire Naturelle" of Paris (p. 129).

Remarks

As stated above about the genus *Loligo*, Lamarck's (1798) paper was based on specimens in the Muséum d'Histoire Naturelle in Paris.
Lamarck's definition of *Loligo vulgaris* is rather concise, in accordance with the taxonomic procedures of his time. Nevertheless, it is sufficient to recognize this species and discriminate it among the four species originally placed in the genus *Loligo*.
It is noteworthy that Lamarck's (1798) definitions of this and the other species is in Latin, whereas those of the genera are in French. One may wonder whether, to Lamarck, the specific entities were more important than the genera.
As for the correct bibliographic reference to cite Lamarck's (1798) paper, see the previous taxonomic item.
Loligo vulgaris was designated type species of *Loligo* by Children (1824), in the sixth and last part of his ponderous work on Lamarck's molluscs. The *Official Index of Names in Zoology* (Anonymous, 2012) erroneously reports 1823 as the publication year ot that part, most probably because the vol. 16 of the journal where it was published extended over the years 1823 and 1824.
Loligo vulgaris Lamarck, 1798 is placed on the *Official List of Generic Names in Zoology* (Anonymous, 2012).

Species *Loligo forbesii* Steenstrup, 1856

Original spelling and combination

Loligo Forbesii (p. 189).

Fig. 2. Portrait of Jean-Baptiste-Pierre-Antoine de Monet chevalier de Lamarck (1744-1829) by Charles Thévenin.

Fig. 2. Jean-Baptiste-Pierre-Antoine de Monet chevalier de Lamarck (1744-1829) ritratto da Charles Thévenin.

Corrected specific name

forbesii (ICZN: art. 28).

Work

J.J.S. Steenstrup, 1856. Hectocotyldannelsen hos Octopodslaegterne Argonauta og Tremoctopus, oplyst ved Iagttagelse af lignende Dannelser hos Blaeksprutterne I Almindelighed. *Det Kongelige Danske Videnskabernes Selskabs Skrifter*, fifth series, 4: 185-216, 2 plts. [In Danish]

Diagnosis (in footnote ** at pp. 189-190)

"Artsmærkerne imellem *Loligo vulgaris Lmck.* og *Loligo Forbesii Stp.* tages bedst af Sugekoppernes Störrelse og Form paa Tentaklerne; disse ere nemlig paa *L. vulgaris* fra Middelhavet, saaledes som *D'Orbigny* og *Verany* beskriver og afbilder dem, og saaledes som de ogsaa gjenlindes hos en Form ved vore Kyster, der vistnok tör ansees for *L. vulgaris*, meget store i de to midterste Rækker og meget smaa i Siderækkerne, saa at disse sidstes Tversnit kun ere Halvparten af de förstes og deres Höide kun en Trediedel af hines, medens hos *L. Forbesii Stp.* de midterste Rækkers Sugeskaale neppe overgaae Siderækkernes i Tversnit og Höide, og det i det Hele seer ud, som om Tentakelköllen havde fire lige store Rækker af Skaale. Sammenlignede med Armenes Sugeskaale ere de midterste Tentakelrækkers Skaaler hos *Loligo vulgaris* 2-3 Gange saa store som de störste Skaaler paa 3die Arm, medens de hos *L. Forbesii* neppe ere en Trediedeel större. — Hornringen i de midterste Rækker af Kopperne hos *L. vulgaris* har kun den ene halve Omkreds fintandet, medens den anden Halvdel er tandlös eller kun bærer en Gruppe af 4-5 smaa butte Tænder (hos vor nordiske Form ere disse endog de eneste Tænder paa Hornringen); hos *Loligo Forbesii* bærer Ringen helt omkring talrige spidse Tænder, i Reglen skiftevis större og mindre. Hos denne have ogsaa Siderækkernes Skaaler Hornringen helt besat med næsten ligestore Tænder, medens hos *L. vulgaris* Hornringen *der* har höie spidse Tænder i den höiere Halvdel og er næsten tandlös i den nedre. I *Farvetegningen* har endnu *L. Forbesii* det Udmærkende, at Farvesækkene forene sig til lange linieformede Pletter eller Striber paa Siderne af Forryggen og ligeledes langs ned med Bugfladens Sider. Disse lange mörke Tegninger og Tentaklernes næsten ligestore Sugekopper adskille saaledes ved förste Öiekast denne Art fra den egentlige *L. vulgaris*. Af begge Arter har jeg fra vore egne Kyster kun kunnet undersöge Hanner; hos os er *L. Forbesii* den almindeligere forekommende og den större. De sædvanlige Exemplarer ere mindst med Tentaklen 24" lange; til Armenes Spidser 20"; til Armenes Rod 15"; Kappen = 1 Fod."

{The specific distinctions between *Loligo vulgaris Lmk.* and *Loligo Forbesii Stp.* are best derived from the size and shape of the suckers on the tentacles; these are for *L. vulgaris* of the Mediterranean as described and illustrated by *D'Orbigny* and *Verany*, and also in a form off our coasts, which one may dare to regard as *L. vulgaris*, very large in the two central rows, and very small in the lateral rows, so that a transverse section of the latter is only one-half of that of the former, and their height only one-third; whilst in *L. Forbesii Stp.* the suckers of the central rows scarcely exceed those of the lateral rows either in transverse section or in height; and, on the whole, it appears as if the club of the tentacle had four equally sized rows of suckers. In comparison with the suckers of the arms, the disks of the central sucker rows of the tentacles in *Loligo vulgaris* are 2-3 times as large as the largest disks on the third arm, whilst in *L. Forbesii* they are scarcely one-third larger. — The horny ring in the central rows of suckers in *L. vulgaris* has only one-half of its circumference finely toothed, whilst the other half is toothless, or only bears a group of 4-5 small blunt teeth (in our northern form these are indeed the only teeth of the horny ring); in *Loligo Forbesii* the ring bears all the way round numerous pointed teeth, and these are as a rule alternately larger and smaller. In this species, also, the suckers of the lateral rows have the horny ring completely set with teeth of almost equal size, whilst in *L. vulgaris* the horny ring has tall pointed teeth in the upper half, and is almost toothless in the lower half. In *colouration* also, *L. Forbesii* has the distinguishing feature of the colour-sacs [i.e. chromatophores] uniting into long linear spots or stripes on the sides of the anterior part of the back, and also down the sides of the ventral surface. These long, dark markings, and the nearly uniform size of the tentacular suckers, consequently separate, at a first glance, this species from *L. vulgaris*. Of both species I have from our own coasts, I only had the opportunity to examine males; here in our waters *L. Forbesii* is the more commonly occurring and the larger. The usual specimens are at least 24" long [ca. 63 cm] with the tentacles; 20" [ca. 52 cm] to the tips of the arms; 15" [ca. 40 cm] to the roots of the arms; the mantle = 1 foot [ca. 31.5 cm].}

Derivation of name

Deonomastic from the family name of the English oceanographer Edward Forbes (1815-1854) in the genitive case: "Jeg har kaldt [...] störste Art [...] *Loligo Forbesii* efter Professor Edward Forbes; jeg har derved villet ikke blot erindre om, at denne Art findes velafbildet i hans ovennævnte fortrinlige Værk, men tillige om denne overordentlig begavede Mands Fortjenester af Naturhistorien i Almindelighed og af vor Kundskab til Havets Dyr i Særdeleshed." (p. 190).

{I have called the largest species [...] *Loligo Forbesii* after Professor Edward Forbes; by doing so, I have wished to keep in remembrance not only that this species is well depicted in his excellent Work, but also the services done by this extraordinarily gifted man to natural history in general and to our knowledge of marine animals in particular.}

Type locality

Danish coasts: "Af begge Arter [i.e. *L. vulgaris* and *L. forbesii*] har jeg fra vore egne Kyster kun kunnet un-

dersöge Hanner" (p. 190) {Of both species [i.e. *L. vulgaris* and *L. forbesii*] I have from our coasts, I only had the opportunity to examine males}.

Type repository

Zoological Museum of the Copenhagen University (fide Sweeney, 2001). Steenstrup was superintendent of this museum (Steenstrup, 1856: footnote at p. 188).

Remarks

Johannes Japetus Smith Steenstrup (**Fig. 3**), was a very bright Danish zoologist, accurate, creative and often fanciful. The latter characteristic also reflected in the organization of his scientific papers. The one in which he described *Loligo forbesii* (Steenstrup, 1856) is a good example for that: despite the fact that his paper was expressly dedicated to the cephalopod hectocotylization, Steenstrup squeezed in it, as a footnote, the description of his new species. Moreover, he did not use the typical "sp. nov." or any equivalent expression to indicate that *L. forbesii* was a new species, although he made it explicit that he himself was its author, by repeatedly placing his abbreviate surname "Stp." after the new binomen. Lastly, Steenstrup (1856: 189) mentioned "hvilken jeg i en anden Afhandling har tillagt Navnet *L. Forbesii Stp.*" {for which I have, in another memoir, proposed the name of *L. Forbesii Stp.*}. It appears that the Danish teuthologist anticipated the discovery of his new loliginid species in a meeting of the Scandinavian Naturalists, whose proceedings were anyway published the year after the publication of the official description of *L. forbesii* as a new species. In fact, in Steenstrup (1857a: 185) we can read that "[...] under the name *Loligo vulgaris*, two species occurred here [i.e. Danish coasts] of which the one was perhaps the genuine *Lol. vulgaris*, but the other a highly different species, *L. Forbesii* Stp." Incidentally, Steenstrup's (1856) paper on hectocotylization was deemed so important by his fellow teuthologists — and indeed it was a wholly original and influential work (Bello, in prep.) — that it was first translated into German and from this language into English (cf. Steenstrup, 1857b).

Fig. 3. Portrait of Johannes Japetus Smith Steenstrup (1813-1897) by August Jerndorff.

Fig. 3. Johannes Japetus Smith Steenstrup (1813-1897) ritratto da August Jerndorff.

Genus *Alloteuthis* Wülker, 1920

Original spelling

Alloteuthis (p. 56).

Work

G. Wülker, 1920. Über Cephalopoden des Roten Meeres. *Senckenbergiana*, 2: 48-58. [In German]

Indication (in list of Loliginidae species; p. 56)

No description is given. Used, in a list of species, as a junior synonym of *Loligo* in combination with the specific name *media* and its Author, thus "13. Loligo (Alloteuthis Naef) media L. [= Linnaeus]."

Derivation of name

Not stated. From *allos* (Greek), different/atypical + *teuthis* (Greek), squid = "atypical squid".

Gender

Feminine.

Type species

Sepia media Linnaeus, 1758, by monotypy.

Other species originally included in the genus

None.

Remarks

In the last half century, this genus authorship has been assigned either to Naef in Wülker (1920) (e.g. Abbott, 1974; Nesis, 1982 and 1987), since Wülker (1920) clearly mentioned Naef as the name's author, or to Wülker (1920) alone (e.g. Voss, 1977; Sweeney & Vecchione, 1998; Jereb et al., 2010). Indeed, according to art. 11.6.1 of the Code (ICZN, 1999), when a name is first published as a junior synonym (i.e. *Alloteuthis*) of a name

then used as valid (i.e. *Loligo*) and afterwards adopted before 1961 as the name of a taxon (such is the case for *Alloteuthis*, extensively used by Naef since 1921), that name is available and dates from its first publication as a synonym but is attributed to that publication's author. See also Sweeney & Vecchione (1998). Accordingly, if *Alloteuthis* was meant by Wülker (1920) as a synonym of *Loligo*, he is to be considered the author of this genus. However, it is not fully clear whether Wülker considered *Alloteuthis* a junior, albeit invalid, synonym or a subgenus. In fact, when citing species synonyms, Wülker (1920) placed them in parentheses, preceded by the equal sign, e.g. "(= Sepia gibbosa Ehrenberg)", which was not the case for *Alloteuthis*, i.e. "(Alloteuthis Naef)" (see above the entry **Indication**); nor there is any suggestion in the text and in subsequent papers by Wülker to solve this puzzle. In the former case, i.e. synonym, the right authorship is to be assigned to Wülker, 1920; in the latter case, i.e. subgenus, the author should be Naef in Wülker, 1920.

In fact, the solution of this problem was provided by Naef himself. The following year, Naef (1921: 535) listed *Alloteuthis* as one of the genera in the family Loliginidae, thus "*Alloteuthis* (Naef MS) Wülker 1920", and further explained that "In meinem MS steht seit 1916 *Alloteuthis*; dieser Name gelangte als Korrektur in einem Separatum an G. Wülker und wurde von ihm (Mai 1920) in den »Ceph. d. roten Meeres« für »*Loligo*« *media* verwandt." {*Alloteuthis* was in my MS [of Die Cephalopoden monograph to be published in 1921-23] since 1916; this name came as a correction in a reprint to G. Wülker and used by him (May 1920) in the »Ceph. d. roten Meeres« [Red Sea cephalopods] for »*Loligo*« *media*}. Moreover, Naef (1923: 195) later on wrote "I used the name *Alloteuthis* already in 1916 in manuscript and reprints from which the name was taken by Wülker, who adopted it (1920, May, p. 56) as a synonym of "*Loligo*" *media* L., which established its nomenclatorial validity." In the latter voluminous work, Naef (1923) described very accurately both the genus *Alloteuthis* and its species (see also **Remarks** to *A. subulata*, below).

To conclude, it is quite evident that the moral authorship of *Alloteuthis* pertains to Naef, even more so because Wülker did not embrace Naef's taxonomical proposal to place the loliginid species *A. media* in a genus apart. Anyway, such a situation does not concern the Code (ICZN, 1999), whose rules appear unfair in the present instance; personally, I believe that this rule of the Code should be modified in order to both disclose the actual history of a generic name and honour the ingenuity of its true author. Naef was deprived of his taxonomic merits more than once; see the case of *Sepiola steenstrupiana* Levy, 1912 / *Sepiola tenera* Naef, 1912 in Bello (2015).

Species *Alloteuthis media* (Linnaeus, 1758)

Work

C. Linnaeus, 1758. *Systema Naturæ. Editio Decima.* Holmiæ [Stockholm], Laurentius Salvius, 824 pp. [In Latin]

Original spelling and combination

Sepia media (p. 659).

Definition (species no. 3 of the genus *Sepia*, in the class Vermes, ordo Mollusca)

"S. corpore depresso caudato-ancipiti." (p. 659)
{Sepia with a body flattened and caudate [i.e. finned] on both sides.}

Derivation of name

Not stated. From *medius* (Latin; feminine: *media*), medium-sized. Probably by comparison with the other four species originally placed in the genus, three of which are larger-sized, namely *Octopus vulgaris* Cuvier, 1797, *Sepia officinalis* and *Loligo vulgaris* (binomina updated according to the current nomenclature), and one is smaller, namely *Sepiola rondeletii* (binomen updated; cf. Bello, 2015).

Type locality

"*Habitat in* Pelago." {It lives in the open sea.} (p. 659).

Type repository

Not specified. Sweeney (2001) reports the Linnean Society of London with a question mark.

Remarks

As usual, the definitions by Linnaeus (1758) are very concise and are not sufficient to discriminate this species from the other four in the Linnaean genus *Sepia*. However, it becomes quite univocal in light of both reference to Rondeletius (1554), thus: "*Rond. pisc.* 508. Loligo parva.", whose figure (Fig. 4) and description refer unmistakably to *A. media* (cf. Naef, 1923), and the diagnosis "*Similis Sepiae officinali, sed latera membrana aucta, quæ membrana affigitur tantum lateribus ad dimidium, nec longitudinalis est*" (Linnaeus, 1758: 659) {Similar to *Sepia officinalis*, but with the lateral fin enlarged, which fin is attached only on the middle of sides, and not lengthwise}.

Species *Alloteuthis subulata* (Lamarck, 1798)

Work

[J.-B.] Lamarck, 1798. *Extrait d'un Mémoire sur le genre de la* Sèche, *du* Calmar *et du* Poulpe, *vulgairement nommés,* Polypes de mer. *Bulletin des Sciences, par la Société Philomatique de Paris.* 1(17): 129-131. [In French; specific definitions in Latin]

Original spelling and combination

Loligo subulata (p. 130).

Definition (species no. 3 of the genus *Loligo*, "3. Calmar subulé. *Loligo subulata*")

"Loligo alis augustis [sic! for angustis] caudae subulatae adnatis, lamina dorsali trinervi utrinque subacuta." (p. 130) {Loligo with narrow wings [= fins] coming out of the subulate tail, lamina [= gladius] with three dorsal nervures, subacute on both sides}

Derivation of name

Not stated. From *subulatus* (Latin; feminine: *subulata*), subulate / awl-like, because of it tapered posterior end.

Type locality

Not stated.

Type repository

"Muséum d'Histoire Naturelle" of Paris (p. 129).

Remarks

As already reported above, the paper by Lamarck (1798) was based on specimens in the Muséum d'Histoire Naturelle in Paris. His definition of *Loligo subulata* is very concise, in accordance with the taxonomic procedures of his time, and might apply to *A. media* as well. Naef (1923), who incidentally deemed not fully warrented all previous records of *A. subulata*, performed an accurate revision of the genus and separated the two species on morphological grounds. He discriminated between *A. media* and *A. subulata* also on the basis of the comparative size of their tentacle clubs. He called *A. media* the species with larger clubs, according to the drawing in Rondeletius (1554) (Fig. 4), which was the reference for the Linnaean *Loligo media* (see above) (cf. Naef, 1923: fig. 100). Since no help can come from the no longer extant type specimen of *A. subulata* (fide Lu et al., 1995), the assignement of either name, *A. media* or *A. subulata*, to either species is currently done in accordance with Naef's (1923) revision. These two species are also separate by genetic analyses (Anderson et al., 2008). Unfortunately, much confusion has occurred in distinguishing the two species – which indeed are not promptly identifiable – in Mediterranean surveys, which in turn brought about uncertainties in their geographic distribution (Lefkaditou et al., 2012). Incidentally, this state of affairs confirms once more the need for a protocol to document cephalopod records (Bello, 2018).

As reported in Remarks to *Loligo vulgaris*, the specific definitions in Lamarck (1798), including the present one, are in Latin language, whereas those of the genera are in French.

As for the correct bibliographic reference to cite Lamarck's paper, see the taxonomic item **Genus *Loligo*** above.

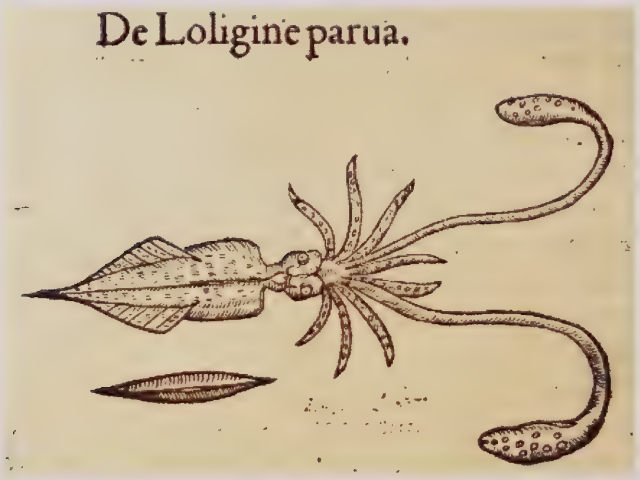


Fig. 4. Guillaume Rondelet's original figure of *Loligo parva* [= *Alloteuthis media*] (after Rondeletius, 1554: p. 508).

Fig. 4. *Loligo parva* [= *Alloteuthis media*], figura originale di Guillaume Rondelet (da Rondeletius, 1554: p. 508).

Discussion

The present paper aimed, in line with Bello (1996, 2015), at providing a documented reference tool for clearing up the nomenclature of the Mediterranean Myopsida taxa and thus fixing some inaccuracies and ambiguities found in the pertinent literature in referring to those taxa. In this respect, the correct bibliographic reference to *Loligo*, i.e. volume of Lamarck's (1798) paper, was indicated. Incidentally, this case shows how mistakes are easily fixed in the taxonomic literature, since it is obvious that researchers have to rely on recent reviews when citing scientific names. That is why systematic lists have to be accurate.

The examination of the entries in the present paper shows the evolution of taxonomic description patterns in just a century, from the too concise Linnaean (1758) and Lamarckian (1798) ones to that very accurate by Steenstrup (1856). It also provides a glimpse of the progress of coleoid systematics in its infancy. Moreover, it may give a look inside the general historical situation, as with the dating and author's naming in the aftermath of the French revolution (see the taxonomic names authored by Lamarck).

Acknowledgementes

I wish to express my gratitude to Dr. Inger Winkelmann for her translation from the Danish of Steenstrup's paper on *Loligo forbesii* and Dr. Ornella Valeria Sapio for her help in translating the Latin definitions. I heartly thank Dr. Fernando Ángel Fernández-Álvarez for his very accurate critical reading of this paper.

References

Abbott R.T., 1974. *American Seashells*, 2nd edition. New York, Van Nostrand Rheinhold, 663 pp.

Allcock A.L., Lindgren A. & Strugnell J.M., 2014. The contribution of molecular data to our understanding of ceph-

alopod evolution and systematics: a review. *Journal of Natural History*, **49**: 1373-1421.

Anderson F.E., Pilsits A., Clutts S., Laptikhovsky V., Bello G., Balgerías E., Lipinski M., Nigmatullin C., Pereira J.M.F., Piatkowski U., Robin J.-P., Salman A. & Tasende M.G., 2008. Systematics of *Alloteuthis* (Cephalopoda: Loliginidae) based on molecular and morphometric data. *Journal of Experimental Marine Biology and Ecology*, **364**: 99-109.

Anonymous, 2012. *Official Index of Names in Zoology – Updated December 2012*. London, The International Trust for Zoological Nomenclature, http://iczn.org/sites/iczn.org/files/Official_List_updated_December_2012.pdf: 804 pp. [accessed 16.6.14].

Bello G., 1996. The original descriptions of the Mediterranean Cephalopods. I: Sepioidea. *Bollettino Malacologico*, **31**: 179-194.

Bello G., 2015. The original descriptions of the Mediterranean taxa in the order Sepiolida (Mollusca: Cephalopoda) with notes on the validity of the specific name *Sepiola rondeletii* Leach, 1817. *Bollettino Malacologico*, **51**: 22-46.

Bello G., 2018. Proposal for a protocol to document cephalopod new records. *Cephalopod International Advisory Council Conference 2018 – November 12-16, 2018, St. Petersburg, Florida, USA*. Book of Abstracts: 99.

Children J.G., 1824. Lamarck's *Genera of Shells*. *The Quarterly Journal of Science, Literature and the Arts*, **16**: 241-264; plt. 6.

Hemming F. (ed.), 1954. OPINION 233 – Suppression, under the Plenary Powers, of the name *Octopodia* Schneider, 1784 (Class Cephalopoda), and of certain reputed names published by the same author in 1784. *Opinions and Declarations rendered by the International Commission on Zoological Nomenclature*, **4**: 275-296.

International Commission on Zoological Nomenclature, 1999. *International Code of Zoological Nomenclature (fourth edition)*. London, The International Trust for Zoological Nomenclature, xxix+306 pp.

Jereb P., Vecchione M. & Roper C.F.E., 2010. Family Loliginidae. In P. Jereb & Roper C.F.E. (eds.), Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Vol. 2. *FAO Species Catalogue for Fishery Purposes*. **4(2)**. FAO, Rome: 38-117.

Lamarck [J.-B.], 1798. *Extrait d'un Mémoire sur le genre de la* Sèche, *du* Calmar *et du* Poulpe, *vulgairement nommés*, Polypes de mer. *Bulletin des Sciences, par la Société Philomatique de Paris*, **1(17)**: 129-131.

Leach W.E., 1817. Synopsis of the Orders, Families, and Genera of the Class *Cephalopoda*. *The Zoological Miscellany*, **3**(30): 137-141.

Lefkaditou E., Corsini-Foka M. & Kondilatos G., 2009. Description of the first Lessepsian squid migrant, *Sepioteuthis lessoniana* (CEPHALOPODA: Loliginidae), in the Aegean Sea (Eastern Mediterranean). *Mediterranean Marine Science*, **10**: 87-97.

Lefkaditou E., Tsigenopoulos C.S., Alidromiti C. & Harlabous J., 2012. On the occurrence of *Alloteuthis subulata* in the Eastern Ionian Sea and its distinction from the sympatric *Alloteuthis media*. *Journal of Biological Research Thessaloniki*, **17**: 169-175.

Lesueur C.A., 1821. Descriptions of several new species of Cuttle-fish. *Journal of the Academy of Natural Sciences of Philadelphia*, **2(1)**: 86-101.

Linnaeus C., 1758. *Systema Naturæ. Editio Decima*. Holmiæ [Stockholm], Laurentius Salvius, 824 pp.

Lu C.C., Boucher-Rodoni R. & Tillier A., 1995. Catalogue of types of recent Cephalopoda in the Museum National d'Histoire Naturelle (France). *Bulletin du Museum National d'Histoire Naturelle de Paris*, **17(A3-4)**: 307-343.

MolluscaBase, 2019. *Loligo* Lamarck, 1798. Accessed through: World Register of Marine Species at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=138139 [15.3.2019].

Naef A., 1921. Das System der dibranchiaten Cephalopoden und die mediterranen Arten derselben. *Mitteilungen aus der Zoologischen Station zu Neapel*, **22**: 527-542.

Naef A., 1923. Die Cephalopoden. *Fauna und Flora des Golfes von Neapel*, **35**(1): 863 pp. [English translation by A. Mercado, 1972; Smithsonian Institution, Washington D.C.: 917 pp.]

Nesis K.N., 1982. *Kraktij opredelitel' golovonogikh molluskov Mirovogo okeana*. Moskow, Legkaya i pishchevaya promyshlennost, 356 pp. [in Russian].

Nesis K.N., 1987. *Cephalopods of the world*. Neptune City, N.J., T.F.H. Publications, 351 pp.

Okutani T., 2015. *Cuttlefishes and Squids of the World (New Edition)*. Tokyo, Tokai University Press, xxvii+247 pp.

Rondeletius G., 1554. *Libri de Piscibus Marinis, in quibus veræ Piscium effigies expressæ sunt*. Lugduni [Lyon], Matthias Bonhomme, pp. vv.+583 pp.

Salman A. & Katagan T., 2002. Lessepsian immigrant cephalopods of the Mediterranean Sea. Workshop on Lessepsian Migration, 20-21 July 2002, Gokceada, Turkey. *Turkish Marine Research Foundation*, **9**: 71-74.

Segawa S., Hirayama S. & Okutani T., 1993. Is *Sepioteuthis lessoniana* in Okinawa a single species? In Okutani T., O'Dor R.K. & Kubodera T. (eds.), *Recent advances in cephalopod fisheries biology*. Tokyo: Tokai University Press: 513-521.

Steenstrup J., 1856. Hectocotyldannelsen hos Octopodslaegterne Argonauta og Tremoctopus, oplyst ved Iagttagelse af lignende Dannelser hos Blaeksprutterne I Almindelighed. *Det Kongelige Danske Videnskabernes Selskabs Skrifter*, fifth series, **4**: 185-216, 2 plts.

Steenstrup J., 1857a. Oplysninger om Atlanterhavets colossale Blæksprutter. *Forhandlinger ved de Skandinaviske Naturforskeres*, **7**: 182-185. [English translation by A. Volsøe, J. Knudsen & W. Rees, 1962; Danish Science Press Ltd., Copenhagen: 330 pp.]

Steenstrup J., 1857b. *Hectocotylus*-formation in *Argonauta* and *Tremoctopus* explained by Observations on similar Formations in the Cephalopoda in general. *The Annals and Magazine of Natural History. 2nd series*. **20**: 81-114; plts. II-III.

Sweeney M.J., 2001. *Current Classification of Recent Cephalopoda*. Washington DC., National Museum of Natural History, www.mnh.si.edu/cephs/ newclass.pdf [accessed 4.2.2011].

Sweeney M.J. & Vecchione M., 1998. Generic and specific names introduced in the squid family Loliginidae (Cephalopoda: Myopsida). In Voss N.A., Vecchione M., Toll R.B. & Sweeney M.J. (eds.), Systematics and Biogeography of Cephalopods. *Smithsonian Contributions to Zoology*, **586**: 223-237.

Vecchione M. & Young R.E., 2016. Myopsida Naef, 1916. Version 29 August 2016. *http://tolweb.org/Myopsida/52670/2016.08.29 in* The Tree of Life Web Project, http://tolweb.org [accessed 25.3.2019].

Voss G.L., 1977. Present status and new trends in Cephalopod systematics. *Symposia of the Zoological Society of London*, **38**: 49-60.

Wülker G., 1920. Über Cephalopoden des Roten Meeres. *Senckenbergiana*, **2**: 48-58.

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Taxonomic and nomenclatural notes on the genus *Idas* (Bivalvia: Mytilidae)

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Abstract
We investigate the generic attribution within Bathymodiolinae of various species of chemosymbiotic mussels. We come to the conclusion that these species belong to the genera *Adipicola* Dautzenberg, 1927 and *Idasola* Iredale, 1915. The two genera, often considered synonyms, present distinct morphological characters of the ligamental area. Additionally, *Idas* Jeffreys, 1876 is pre-occupied by *Idas* Mulsant, 1875 (Aves) and we thus suggest its replacement with *Idasola* Iredale, 1915.

Key Words
Mytilidae, *Idas*, *Idasola*, *Adipicola*, taxonomy.

Riassunto
Sulla base delle morfologie conchigliari, gli Autori disquisiscono a quali generi di Bathymodiolinae vadano riferite le varie specie di mytilidi chemosinbiotici presenti in particolare nel Mediterraneo. Malgrado i complessi problemi nomenclaturali e tassonomici giungono alla conclusione che queste specie vanno inquadrate nei generi *Adipicola* Dautzenberg, 1927 e *Idasola* Iredale, 1915. I due generi, sovente ritenuti sinonimi, presentano infatti caratteri morfologici dell'area legamentare assolutamente distinti. Dall'analisi della bibliografia appare inoltre indiscutibile che *Idas* Jeffreys, 1876 è preoccupato da *Idas* Mulsant, 1875 (Aves) e che pertanto è giustificata la sua sostituzione con *Idasola* Iredale, 1915.

Parole chiave
Mytilidae, *Idas*, *Idasola*, *Adipicola*, tassonomia.

Introduction

In a recent paper on the deep-sea chemosymbiotic mussels of the Mediterranean, Giusti et al. (2012) express themselves in favor of maintaining, as a reference at the overspecific level, the only genus *Idas* Jeffreys, 1876, still considering insufficiently proved the differences from the conchigliological point of view, constant and taxonomically relevant, between *Idas* Jeffreys and *Adipicola* Dautzenberg, 1927. Earlier also Warén (1991) and Pelorce & Poutiers (2009) had expressed a similar opinion while Bodwen & Heppel (1966), Dell (1987), Gustafson et al. (1998), Huber (2010), Lorion et al. (2010), Ockellmann & Dinesen (2011) and Ritt et al. (2012) decided to keep the two genera separate. While CLEMAM considers the only genus *Idas*, WoRMS keeps separate *Idas* and *Adipicola*, besides *Habepegris* Bernard, 1978, generally considered, the latter, synonymous with *Idas*; the problem therefore remains open.
There is a second problem: the genus *Idas* s.l. has had a complex history from the taxonomic and nomenclatural point of view, with at least seven different possible synonyms but, in our opinion, its formal validity has not yet been convincingly resolved. Iredale (1915), in fact, recognizes that *Idas* Jeffreys, 1876 is worried by *Idas* Mulsant, 1875 (Aves); therefore proposes the new name *Idasola* to replace *Idas* Jeffreys. Some authors, such as Vokes (1967), Bernard (1978), Warén (1991, 1993), Poppe & Goto (1993), Huber (2010), nevertheless consider *Idas* Mulsant nomen nudum for which they reject the motivations of Iredale, therefore considering superfluous the name *Idasola*. This approach is generally accepted even if they express differently, among others, Soot-Ryen (1955), van Regteren Altena (1964), Bodwen & Heppel (1966), Habe (1976) and above all Dell (1987).
The careful reading of the bibliography and the availability of a large number of specimens of chemosynthetic mussels dredged in the upper Tuscan Archipelago between 500 and 700 meters deep, including specimens in various stages of development belonging to all species known for the Mediterranean (cf. Giusti et al., 2012) and others in the course of study, allowed a series of observations that, in our opinion, can offer a contribution to a possible solution to the problems outlined.

Materials and methods

The material examined for this work comes from sediments rich in organic material and sunken wood recovered from vessels between 500 and 700 meters deep in the Tuscan Archipelago and, in particular in the area between the lower Ligurian Sea and the upper Tyrrhenian Sea. From these sediments several hundreds of isolated valves and/or specimens with valves in anatomical connection and/or live specimens have been separated. Much of this material is being studied at the level of specific definition.

The material was examined with the optical stereomicroscope and for some details related to the ligament areas, through the ESEM, the latter available at the CUGAS of the Padova University.
The direct examination of the bibliography, especially the less recent one, was fundamental to clarify some points related to the intricate taxonomic and nomenclatural questions addressed.
Acronims: MSNM-Li = Museo di Storia Naturale del Mediterraneo della Provincia di Livorno, B.D.c. = Bruno Dell'Angelo collection, P.M.c. = Paolo Mietto collection, L = length of the shell, H_u = hight of the shell at level of the beak, H_m = maximum hight of the shell.

Systematic

Dell (1987) reconstructs in a very effective way, albeit with some inaccuracy, the complex taxonomic history of the deepwater chemosynthetic mussels, historically included in the subfamily Bathymodiolinae Kenk & Wilson, 1985. In our opinion, retrace this route chronologically:

Myrina H. & A. Adams, 1854; type-species *Myrina denhami* H. & A. Adams, 1854 for monotypy. This species, however, had already been described by Woodward (1854) as *Modiolarca? pelagica*. The same H. & A. Adams (1857) seem to recognize this synonymy. Dell (1987) recognizes the latter as a type-species of *Myrina* but, as Warén (1991) points out, this annotation, regardless of synonymy, is obviously incorrect. An element of great taxonomic value is that, in the original description, H. & A. Adams (1854) indicate for *Myrina* the presence of an internal ligament.

Idas Jeffreys, 1876, type-species *Idas argenteus* Jeffreys, 1876 for monotypy. An element of great taxonomic value is that, in the original description, Jeffreys (1876) indicates for *Idas* the presence of an external ligament. The genus *Idas* has been accepted by many authors including Verrill (1882), Smith (1885, 1904), Vokes (1967), Bernard (1978), Waren (1980, 1991, 1993), Warren & Carrozza (1990), Sabelli et al. (1990), Poppe & Goto (1993), Arduino et al. (1995), Salas (1996), Gustafson et al. (1998), Giannuzzi-Savelli et al. (2001), Repetto et al. (2005), Kiel & Goedert (2007), Pelorce & Poutiers (2009), Oliver & Holmes (2009), Huber (2010), Tylor & Glover (2010), Cossignani & Ardovini (2011), Gofas et al. (2011), Ockelmann & Dinesen (2011), Janssen & Krylova (2011), Giusti et al. (2012), Gaudron et al. (2012), Ritt et al. (2012), Laming et al. (2014), Rodrigues et al. (2015), Alf & Haszprunar (2015), Danise et al. (2016), Amon et al. (2016).

Idasola Iredale, 1915, name introduced by Iredale to replace *Idas* Jeffreys as the latter was pre-occupied by *Idas* Mulsant, 1875 (Aves). The type-species of *Idasola* therefore remains *Idas argenteus* Jeffreys, 1876. Vokes (1967) corrects to 1876 the date of the paper of Mulsant and also defines *Idas* Mulsant as nomen nudum. In his opinion, therefore, *Idasola* Iredale is completely superfluous. Bernard (1978) is also of the same opinion. Dell (1987) disputes the opinion of Vokes because, in the paper of Mulsant (1876), the new genus *Idas* is accompanied by the definition of the type-species "*magnificus* Vieillot". As reported by Dell (1987), this species of hummingbirds, contrary to what was stated by Warén (1991), is actually listed in the Peters Catalog (1945: p. 31) as *Lophornis magnifica* (Vieillot) (= *Trochilus magnificus* Vieillot 1817). According to Dell (1987) there are, therefore, all the conditions required by the I.C.Z.N. to validate the name of Mulsant, being a generic name introduced before 1931 (Article 12). [The examination by the writers of the paper of Vieillot (1817) has been confirmed the correctness of the description of *Trochilus magnificus*, thus confirming the formal validity of the genus *Idas* Mulsant]. Warén (1991) does not dispute the latter observation of Dell (1987) but points out that while Jeffreys' paper appeared in the November 1876 issue of the Annals and the Magazine of Natural History, instead of a precise date of Mulsant's paper this must be brought back to December 31, 1876.
At this point Jeffreys' paper would have priority over Mulsant's. Dell (1995) seems to welcome Warén's interpretation, but the situation is more complex: there are in fact three papers by Mulsant that refer to the genus *Idas*, Mulsant, 1875 (p. 27: *Idas*, species *magnificus* Vieillot), Mulsant, 1876 (p. 223: *Idas*, species *magnificus* Vieillot), Mulsant & Verreaux, 1876 [p. 211, species = *Idas magnificus* Vieillot; *Trochilus magnificus* (Vieillot, 1817)]. Although the paper of Mulsant, 1875 is almost identical to the one published in 1876 in the Annales de la Société Linnéenn del Lyon et des Société Botanique de Lyon, the former paper is different only for the page numbering. In fact, this paper was published in 1875 as separate, as reported in the catalog of the French scientific bibliography published by the Ministére de l'Interieur (1875: pp. 755-756) and then valid on the basis of the article 21.8.1. of I.C.Z.N.
It therefore appears that, as correctly indicated by Iredale (1915) the date of establishment of *Idas* Mulsant is 1875 and not 1876 and therefore prior to the establishment of *Idas* Jeffreys. For our part we therefore believe that the replacement of *Idas* Jeffreys, 1876 by *Idasola* Iredale 1915 is formally acceptable on the basis of the provisions of the ICZN. In this regard Warén (1991) notes "*In order to follow you ICZN, JEFFREY'S name should be kept (as did VOKES 1980), especially since this does not disturb the present nomenclature hummingbirds.*"
But this, however qualified, is the writer's opinion that, on the basis of the above, we do not feel like sharing. In fact, the stability of the nomenclature could be invoked if *Idasola* was a name rarely cited and only in the past, something that does not correspond to reality at all, suffice it to mention the papers of Bodwen & Heppel (1966) which correctly report the date of establishment of *Idas* Mulsant, in addition to Dell (1987), Sabelli et al. (1900), Arduino et al. (1995) Goedert et al. (1995), Giannuz-

zi-Savelli et al. (2001), Repetto et al. (2005) and Kiel & Goedert (2006).

Adipicola Dautzenberg, 1927 nomen novum pro *Myrina* H. & A. Adams, 1854 pre-occupied by *Myrina* Fabricius, 1808 (Lepidoptera). The curious name chosen by Dautzenberg refers to the fact that the mollusks [*Adipicola pelagica* (Forbes) Woodward] examined were adherent to a floating block of whale fat. And here arises a problem as Woodward (1927: pp. 274) erroneously credits the institution of the genus *Myrina* H. & A. Adams to 1857. In this paper, H. & A. Adams (1857: p. 514) seem to recognize the synonymy between their *Myrina denhami* and *Modiolarca? pelagica* Woodward indicating with the new *Myrina pelagica* combination. It is for this reason that Dell (1987), recognizing the synonymy but not mentioning in the bibliography the paper of H. & A. Adams (1857), credits *Myrina pelagica* as a type-species of *Adipicola*. It is however very strange that neither Dautzenberg (1927) nor Dell (1987) nor Warén (1991) mention the true type-species of *Myrina* which, by original definition, is in fact *Myrina denhami*, almost as the paper of H. & A. Adams of 1854 in which *Myrina* was erected, had not been taken into actual examination. It is Dell (1995: p. 4), however, which correctly mentions *Myrina denhami* H. & A. Adams, 1854 as a type-species of *Adipicola*.
In the synonymy of *Adipicola pelagica*, finally, Dautzenberg (1927: pp. 274-275) also raises *Myrina dalmasi* Dautzenberg & Fisher, 1897. After the examination of the original material, this synonymy is also accredited by Warén (1991: page 116).
Many Authors, among them in particular Warén (1991, 1993), Pelorce & Poutiers (2009), Giusti et al. (2012), Gofas et al. (2011) and CLEMAM, have considered at least premature the separation between *Idas/Idasola* and *Adipicola*; other malacologists, among them Bodwen & Heppel (1966), Dell (1987, 1995), Gustafson et al. (1998), Tunncliffe et al. (1998), Smith & Baco (2003), Southward (2008), Chambers & Sowerby (2009), Duperron (2010), Lorion et al. (2010, 2012), Huber (2010), Ockelmann & Dinesen (2011), Ritt et al. (2012), Samadi (2014), Danise et al. (2016), Danise et al. (2016), Signorelli & Crespo (2017), as well as WoRMS, have instead supported the opportunity, based on both shell morphology and on the anatomy of the soft parts and on a molecular basis, and on ecological considerations, to keep the two separate taxonomic entity in question.

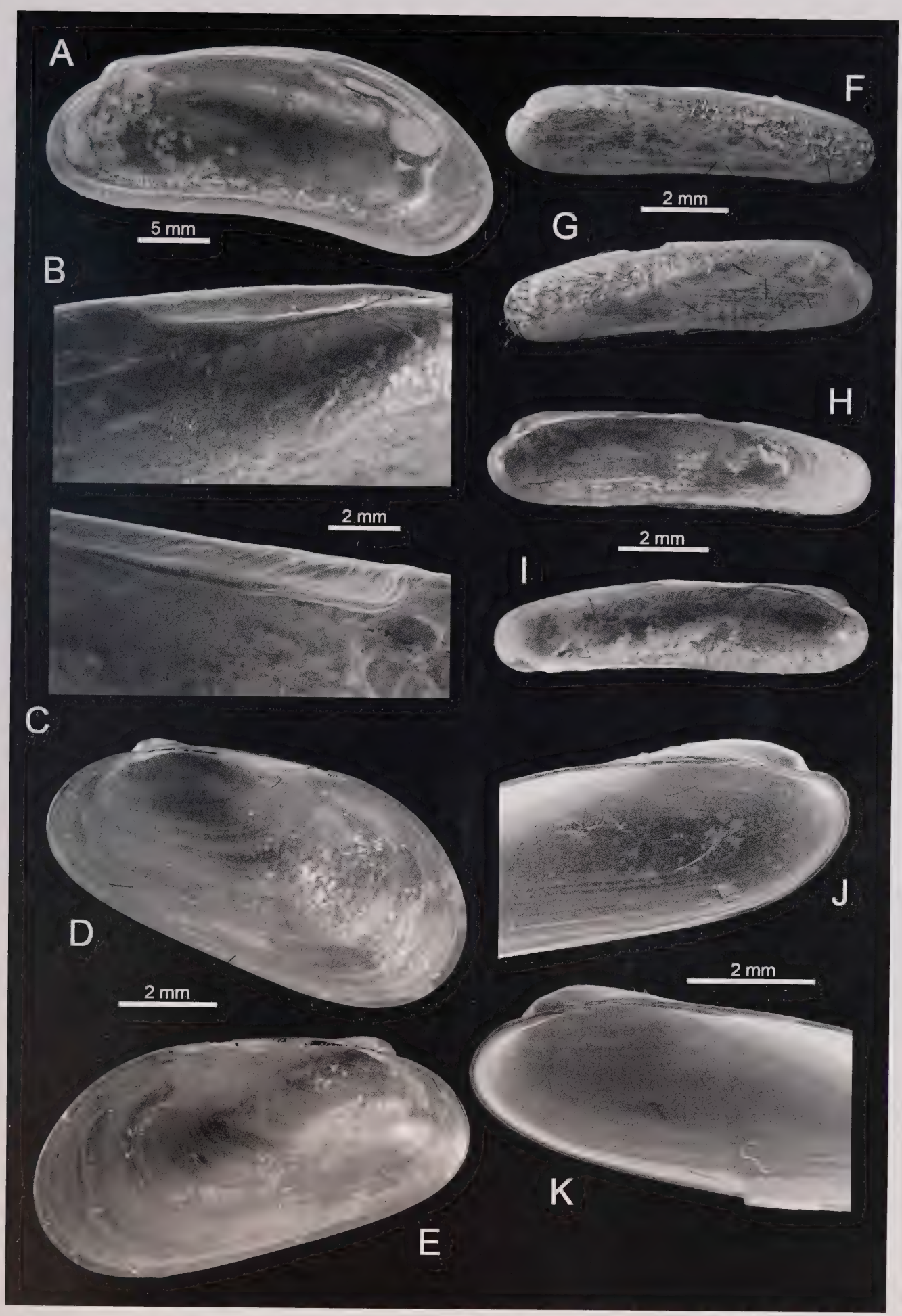
Terua Dall, Bartsch & Rehder, 1938, type-species *Terua pacifica* Dall, Bartsch & Rehder, 1938. This combination, although credited by Habe (1977) and Koruda, Habe & Koyama (1981) [the latter paper erroneously mentioned in Dell (1987) as Habe (1981)] is disputed by Dell (1987) which recognizes, due to the morphological characteristics, the belonging of *Terua pacifica* to the genus *Adipicola*. The genus *Terua* is therefore placed in synonymy with *Adipicola*. This approach is accepted by Warén (1991) even if, as described above, with reference to the genus *Idas*. Dall, Bartsch & Rehder (1938) report that they did not find the species in question associated with organic material and Dell (1987) considers this fact as a possible anomaly of *Adipicola*. In this regard, however, we would like to point out that, in the material we have collected, the presence of specimens, even with valves in anatomical connection, is occasional even in sediments without organic material.

Myridas Iredale, 1939 nomen novum pro *Myrina* H. & A. Adams, 1854 not Fabricius, 1808 (Lepidoptera); type-species as *Myrina coppingeri* Smith, 1885. It is evident that Iredale (1939) did not know the previous paper of Dautzenberg (1927) that substituted for the same reason *Myrina* H. & A. Adams with *Adipicola*. *Myridas*, however, can not be considered synonymous with *Adipicola* as *Myrina coppingeri*, due to the characteristics of the ligament, is to be relocated to *Idasola*, as demonstrated by Dell (1987).

Myrinopsis Nordsieck, 1969 as a subgenus of *Adipicola* Dautzenberg, 1927; type-species *Myrina modiolaeformis* Sturany, 1896 for monotypy. According to Dell (1987), the Sturany species can be classified as *Idas/Idasola* even if it does not exihibit periostracal hairs, a character that according to Huber (2010) characterizes the genus *Adipicola*. However, the situation is more complex. Warèn (1991: figs 41 A-C) illustrates the Sturany syntypes. In particular, fig. 41C shows the posterior area in which appears an elongated and slightly spatulate ligamental layer that corresponds to what is illustrated by Giusti et al. (2012: figs. 2 K-L). One of the Sturany syntypes, kept at the Naturhistorishe Museum in Wien, was recently also illustrated by Albano et al. (2018: fig. 10. A, C, H), in which this evidence is however less marked. Also Giannuzzi -Savelli et al. (2001) show in fig. 232a a paratype (sic!) of *Idas modiolaeformis* of the series of Sturany syn-

Fig. 1. A. *Adipicola simpsoni* (Marshall, 1900), specimen K in Giusti et al. (2012), P.M.c., right valve, inner view. **B.** *A.* cf. *simpsoni* (Marshall, 1900), specimen J in Giusti et al. (2012), P.M.c., right valve, particular of the posterior ligamental area. **C.** *A. simpsoni* (Marshall, 1900), specimen 66, P.M.c., left valve, particular of the posterior ligamental area. **D-E.** *Adipicola modiolaeformis* (Sturany, 1896), specimen C in Giusti et al. (2012), P.M.c., **D.** right valve, inner view, **E.** left valve, inner view. **F-G.** *Idasola cristiani* (Giusti, Mietto & Sbrana, 2012), specimen of B.D.c. in Giusti et al. (2012), **F.** left valve, outer view, **G.** right valve, outer view, **H.** right valve, inner view, **I.** left valve, inner view. **I-K.** *Idasola emmae* (Giusti, Mietto & Sbrana, 2012), holotype of MSNM-Li 736 (courtesy of Antonio Borzatti de Loewenstern), **I.** left valve, particular of the posterior ligamental area, **K.** right valve, particular of the posterior ligamental area.

Fig. 1. A. *Adipicola simpsoni* (Marshall, 1900), esemplare K in Giusti et al. (2012), P.M.c., valva destra, vista interna. **B.** *A.* cf. *simpsoni* (Marshall, 1900), esemplare J in Giusti et al. (2012), P.M.c., valva destra, particolare dell'area legamentare posteriore. **C.** *A. simpsoni* (Marshall, 1900), P.M.c., esemplare 66, valva sinistra, particolare dell'area legamentare posteriore. **D-E.** *Adipicola modiolaeformis* (Sturany, 1896), esemplare C in Giusti et al. (2012), P.M.c., **D.** valva destra, vista interna, **E.** valva sinistra, vista interna. **F-G.** *Idasola cristiani* (Giusti, Mietto & Sbrana, 2012), esemplare in B.D.c. in Giusti et al. (2012), **F.** valva sinistra, vista esterna, **G.** valva destra, vista esterna, **H.** valva destra, vista interna, **I.** valva sinistra, vista interna. **I-K.** *Idasola emmae* (Giusti, Mietto & Sbrana, 2012), olotipo in MSNM-Li 736 (cortesia di Antonio Borzatti de Loewenstern), **I.** valva sinistra, particolare dell'area legamentare posteriore, **K.** valva destra, particolare dell'area legamentare posteriore.


A
5 mm
B
2 mm
C
D
2 mm
E
F
2 mm
G
H
2 mm
I
J
2 mm
K

types. The morphometric parameters of this specimen - which corresponds to that illustrated by Albano et al. (2018) - and in particular the L/H_u and L/H_m relations respectively 2.20 and 1.76 coincide well with those of Giusti et al (2012: figs 2 HI), respectively 2.14 and 1,80.
Giannuzzi-Savelli et al. (2001: Fig. 234b) also illustrate a second example from the Medinaut Expedition and also identified as *Idas modiolaeformis*. This is a specimen isolated from a large stock of forms found south of Crete at depths between 1700 and 2000 m and so also identified in Olu-le-Roy et al. (2004). This data was also reported by Fiala-Mèdioni (2003) and by Southward et al. (2011) and is compatible with what reported by Gaudron et al. (2012) and Luming et al. (2014). However, it is a form that has different parameters from those of the Sturany sintype ($L / H_u = 2.37$, $L / H_m = 2.00$) but above all exhibits periostracal hairs, which are completely missing in the original material (Sturany, 1896; Dell, 1985; Warèn, 1991), and in accordance with the opinion of Ritt et al. (2012) and Giusti et al. (2912). It is therefore a different species that, at an initial iconographic examination, seems to fit into the group of *Idas argenteus* Jeffreys, 1876 and *Idas lamellosus* Verrill, 1885. Pelorce & Poutiers (2009) report that studies on endosymbiotic chemosynthetic bacteria (Duperron, 1995) and molecular analysis in progress by J. Lorion, indicate an affinity between the former specimens and *"Idas" macdonaldi* Gustafson, Turner, Lutz & Vrijenhoek, 1998. But *"Idas" macdonaldi*, in addition to being free of periostracal hairs, presents a ligamental area which is typical of *Adipicola* and not of *Idas/Idasola* as it seems to suggest the example illustrated by Giannuzzi-Savelli et al. (2001: Fig. 234 b) and from Olu-le-Roy (2004: Fig. 3 in the upper left). It is therefore possible that the stock collected during the Medinaut Expedition is not homogeneous from the taxonomic point of view.
The conformation of the ligamental area detectable in the syntype and in the material of the Tuscan Archipelago attributed to *Idas modiolaeformis* by Giusti et al. (2012) suggests attributing the species under investigation to *Adipicola*, therefore, *Myrinopsis* is junior synonymous, as believed on another basis by Huber (2010).
The binomial *Adipicola modiolaeformis*, however, had already been used by Nordsieck (1967), Parenzan (1934), Piani (1980), Bruschi et al. (1985), Sabelli et al. (1990), Poppe & Goto (1993), Arduino et al. (1995), and Cossignani & Ardovini (2011).

Habepegris Bernard, 1978; type-species *Habepegris washingtoniana* Bernard, 1978. Although Ockelmann & Dinesen (2011) and WoRMS accredit this as a valid genus, there is no justification for not considering *Habepegris washingtoniana* afferent to *Idas/Idasola* (see also Lorion et al., 2010, 2012). In the original definition, in fact Bernard (19078) states that *H. washintoniana* does not have periostracal bristles and shows evident denticulations along the posterior margin. In the examination of the original material, Dell (1987), on the other hand, monitors the periostracal hairs and does not notice morphological characteristics such as to justify the creation of a new genus, an opinion reiterated also in Dell (1995). Also *Habepegris* is therefore to be considered junior synonym of *Idas/Idasola*.

Adula H. & A. Adams, 1857; type-species *Mytilus soleniformis* d'Orbigny, 1857. The reference to this genus of mytilide lithophagide - not therefore belonging to the so-called Bathymodiolinae (see Ockelmann & Dienesen, 2009), is a must since Marshall (1902) - Dell (1987: p 18) makes inaccurate reference to Marshall 1901, which he considers influenced, in his taxonomic elaborations, by Smith - modifies the generic attribution of *Myrina simpsoni* Marshall 1900, precisely in *Adula (Myrina) simpsoni*. Both Lamy (1937) and Tebble (1966) approve this relocation so much that the latter author considers both *Idas* and *Adipicola* synonyms of *Adula*. Before Warén (1990) demonstrated the inconsistency of this attribution - in spite of the similar ligamental area structure (see Ockelmann & Dinesen, 2009) - many authors (Nordsieck, 1969; Barsotti, 1972; Quero, 1973; Barsotti & Giannini, 1974; Piani, 1980; Terreni, 1981; Carrozza, 1984; Bruschi et al., 1985; Berrow et al., 1995) have adopted the binomial *Adula simpsoni*. While Sabelli et al. (1900), Arduino et al. (1995) Giannuzzi-Savelli et al. (2001) and Repetto et al. (2005) used the binomial *Idasola simpsoni*, most of the authors (Warén & Carrozza, 1990; Waren, 1991; Poppe & Goto, 1993; Ardovini & Cossignani, 1999; Bolotin et al., 2005; dubiously Pelorce & Poutiers, 2009; Huber, 2010; Taylor & Glover, 2010; Cossignani & Ardovini, 2011, Janssen & Krylova, 2011) reported the Marshall species to the genus *Idas*. Only Oskarsson (1982), Dell (1987) Smith & Baco (2003: as *Idas (Adipicola) simpsoni*) and finally, Allen (2008) and Chambers & Sowerby (2009) attribute *Myrina simpsoni* to the genus that we too, on the basis of the characters of the ligamental area, consider correct for this species, i.e. *Adipicola*. As we will see later, the posterior ligamental area - which Dell (1987) considers to be comparable with that of the genus *Philobrya* Carpenter, 1872 - is fully compatible with what is observed in *Adipicola*.

Class Bivalvia Linnè, 1758
Subclass Pteromorphia Beurlen, 1944
Superfamily Mytiloida de Fèrussac, 1822
Family Mytilidae Rafinesque, 1815
(Subfamily Bathymodiolinae Kenk & Wilson, 1985)
Genus *Adipicola* Dautzenberg, 1927

type-specie: *Myrina denhami* H. & A. Adams, 1854
(= *Modiolarca ? pacifica* Woodward, 1854)

Myrina – H. & A. Adams, 1854: p. 76.
Terua – Dall, Bartsch & Rehder, 1938: p. 57.
Myrinopsis – Nordsieck, 1969: p. 31.

Amended diagnosis

Inequilateral shell with a subtrapezoidal subrectagular

shape, sometimes very elongated with respect to height, with the anterior part always less high than the posterior. In some species the posterior part is curved with respect to the dorsal margin which is straight. Periostracum smooth, shiny, often overflowing, normally free of periostracal hairs, sometimes with a very fine feltration in the middle part of the ventral area. Ornamentation given by large and irregular striations of growth sometimes interrupted by evanescent traces of vertical stripes. Hinge consists of an antero-cardinal area with a series of small vertical denticulations located immediately below the beak and a series of crenulations along the posterior margin. Elongated opistodetic ligament allocated in a more or less spatuliform layer located below the posterior crenulations. The latter, during the ontogenetic development, become more and more obsolete until they are covered by an extensive callosity. In some species, however (see Dell, 1985) the crenulations begin just above the distal termination of the legamental layer and then extend to the distal part of the posterior margin. Prodissoconc small, generally colorless with the shell; however, in some species, such as in *Adipicola simpsoni*, it is evident, also on a chromatic basis, the separation between prodissoconch I and prodissoconch II. The dimensions vary from species to species up to a maximum shell length of 40 mm and maximum hight of about 17 mm (*Adipicola simpsoni*).

Composition of the genus (living species)

Modiolarca? pacifica Woodward, 1854; *Myrina modiolaeformis* Sturany, 1896; *Myrina simpsoni* Marshall, 1900; *Modiola projecta* Verco, 1908; *Modiolus dubius* Prashad, 1932; *Terua pacifica* Dall, Bartsch & Rehder, 1938; *Terua crypta* Dall, Bartsch & Rehder, 1938; *Myrina longissima* Thiele & Jaeckel, 1932; *Adula iwaotakii* Habe, 1958; *Adipicola osseocola* Dell, 1987; *Adipicola arcuatilis* Dell, 1995; *"Idas" macdonaldi* Gustafson, Turner, Lutz & Vrijenboek, 1998; *"Idas" cylindricus* Pelorce & Poutiers, 2009; *Adipicola leticiae* Signorelli & Crespo, 2017.

Observations

From the conchigliological point of view, *Adipicola* is distinguished from *Idasola* for the morphology of the ligamental area that in *Adipicola* is characterized by a ligament allocated in a characteristic layer placed under the posterior crenulation thus simulating an internal ligament; in *Idasola*, however, the posterior ligament is decidedly external. *Adipicola* should also be compared with *Benthomodiolus* Dell, 1987 which is distinguished by the lack of periostracal hairs and a different structure of detracting muscles (Dell, 1985: figs 42 and 50-53). Huber (2010) considers the presence/absence of periostracal hairs a distinctive element between *Idas* (vel *Idasola*) and *Adipicola*. We do not agree with this interpretation for at least two reasons. First of all, if this character assumes primary value, it should be applied to the whole Mytilidae family, but it is not. In fact, to cite an example, within the genus *Modiolus* Lamarck, 1799, we find both the type-species *Modiolus modiolus* (L., 1754), without periostracal hairs, and *Modiolus barbatus* (L., 1758) which is instead provided with, nor is it ever justified to create a new genus for the latter species. Among the material under study by the writers we also have evidence of various examples referable to the genus *Adipicola*, on the basis of the ligamental area, but provided with periostracal hairs. This character, therefore, and in accordance with Dell (1985) is secondary and is therefore important from a taxonomic point of view but only at a specific level. Following the suggestions of Moore (1969) and Yonge (1978) we therefore attribute, in this case, a primary taxonomic value to the only characters of the ligamental area.

Distribution

The genus is present in all the seas of the world at depths between 300 and over 2500 m. In the Mediterranean, the species *Adipicola modiolaeformis* (Sturany, 1896), *A. cylindricus* (Pelorce & Poutiers, 2009) and *A. simpsoni* (Marshall, 1900) are currently recognized.

Paleontology

The presence of the visible spatuliform ligament layer that can be observed in *Idas? olimpicus* Kiel & Goedert (2007), from Eocene-Oligocene beds of the Olympic Peninsula (California, US), allows to refer the species to the genus *Adipicola*.
As also reported by Goedert et al. (1994), and by Kiel & Goedert (2006) these specimens come from the fossil whales community of the Makah and Pysht Formations. *Adipicola olimpica* should be considered the oldest representative of the genus. In agreement with Goedert et al. (1994), in fact, *Idasola? bakeri* (Dickerman) of the Paleocene of California does not refer to mussels (Moore, 1983).
From the Langhian of Caselle di Romagnano near Carpineti (Reggio Emilia, Italy), associated with fossil bones of toothed whales comes *Adipicola appenninica* Danise, Bertolaso & Dominici (2016). Although it is not visible, in the illustrated material, the inner part of the valves appears highly justifiable, due to the general shape of the shell, its attribution to *Adipicola*; this opinion is also confirmed by WoRMS.
Still WoRMS credits to *Adipicola* the species of the lower Middle Miocene of Hokkaido (Japan) originally described as *Adula chikubetsensis* Amano (1994). Also in this case the generic attribution is based on the external shell form and morphology. Like all fossil species attributable to this genus, also *Adipicola chikubetsensis* comes from the whale-fall community (Amano & Little, 2005; Amano et al., 2007).
Finally, for the characteristics of the ligamental area, *Idasola lignicola* (Janssen, 1972: pp. 14-16, text-fig. 2, pl, 2, fig. 1) described from the middle miocenic Twistringer Schichten of Antwerpen-Berchem (Belgium) and Twistringer (Germany), is to be assigned to *Adipicola*.

Genus *Idasola* Iredale, 1915

type-species: *Idas argenteus* Jeffreys, 1876

Idas – Jeffreys, 1876: p. 428
Myridas – Iredale, 1939: p. 425.
Habepegris – Bernard, 1978: p. 63.

Amended diagnosis

Shell of subrectangular-rhomboidal shape more or less elongated with beaks strongly displaced towards the anterior border. The dorsal margin is straight while the ventral is depressed in the middle. In some species the back of the shell is also strongly deflected, causing the shell to have a more or less curved shape. In these cases there is a low hull that pushes towards the postero-ventral margin from the beak. Glossy, often overflowing periostracum, normally covered by periostracal hairs. The latter, based on a typical triangular shape (see Giusti et al., 2012) are generally more numerous along the eventual hull and in any case in the rear portion of the shell. The color of the periostracum can vary from silvery white to brownish. Ornamentation consisting of dense and more or less regular growth streaks, sometimes with slender traces of vertical stripes. Hinge consists of an anterior-cardinal area with a series of small vertical denticulations located immediately below the beak and a series of slender crenulations that can also extend along the entire posterior margin. Elongated opistodetic ligament allocated in a thin groove that develops above or sideways to the posterior crenulations. In the latter case the ligament is partly overlapping the crenulations. Prodissoconch small, not always colorless with the shell; however, in some species, it is evident, also on a chromatic basis, the separation between prodissoconch I (generally darker) and prodissoconch II (typically color as periostracum).
The dimensions vary from species to species up to a maximum shell length of a little more than 20 mm and maximum hhight of about 10 mm (*Idasola japonica* fide Dell. 1987).

Composition of the genus

Idas argenteus Jeffreys, 1876; *Idas lamellosus* Verrill, 1882; *Myrina coppingeri* Smith, 1885; ? *Idas dalli* Smith, 1885; *Myrina indica* Smith, 1904; *Idasola japonica* Habe, 1976; *Habepegris washingtonia* Bernard, 1978; *Idas ghisottii* Warén & Carrozza, 1990; *Idas cristiani* Giusti, Mietto & Sbrana, 2012; *Idas emmae* Giusti, Mietto & Sbrana, 2012; *Idas filippoi* Giusti, Mietto & Sbrana, 2012; *Idas jaclinae* Giusti, Mietto & Sbrana, 2012.

Remarks

As highlighted above, *Idasola* distinguishes itself from *Adipicola* due to the presence of a rear ligamental area decidedly placed in an external position. According to Dell (1985), *Idasola* is separable from *Benthomodiolus* both for the characters of the ligamental area (presence of crenulations of which *Benthomodiolus* is lacking) and for the shape of the retractor muscle. Regarding the presence of periostracal hairs, please refer to what is written in relation to *Adipicola* but it is important to point out the fact that specimens were isolated from the material being studied, attributable to the characteristics of the *Idasola* ligamental area, but without periostracal hairs.

Distribution

Idasola is documented in all the seas of the world at depths between 300 and over 2500 m. In the Mediterranean are currently documented the species *Idasola ghisottii* (Warén & Carrozza), *I. cristiani* (Giusti, Mietto & Sbrana, 2012), *I. emmae* (Giusti, Mietto & Sbrana, 2012), *I. filippoi* (Giusti, Mietto & Sbrana, 2012) and *I. jaclinae* (Giusti, Mietto & Sbrana, 2012).

Paleontology

At present, no report confirms the presence of the genus *Idasola* before the current one.

Conclusions

The careful analysis of the bibliography and the application of the ICZN rules make it possible to consider the replacement of *Idas* Jeffreys, 1876 with *Idasola* Iredale, 1915 fully justified. The presence of an extended ligamental layer developed below the crenulations marking the posterior margin of the shell is a character that is found only in the genus *Adipicola* Dautzenberg, 1927, a character that instead lacks entirely in *Idasola*. It is believed that this is the only constant shell's character that differentiates the two genera, both documented in the Mediterranean. This opinion is in tune, from the conchigliological point of view, with the conclusions reached by Gustafson et al. (1998), analyzing the characteristics of the soft parts, and on a molecular and evolutionary basis by Lorion et al. (2010, 2012) and Samadi (2014).

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Bibliography

Adams H. & Adams A., 1854. Description of a new genus of bivalve Mollusca. *The Annales and Magazine of Natural History, including Zoology, Botany and Geology*, **14** (2): 76.

Adams H. & Adams A., 1857. *The genera of recent Mollusca; arranged according to their organization.* Vol. 2. van Voorst, London, 413-540 pp.

Albano P.G., Schnedl S.-M. & Eschner A., 2018. An illustrated catalogue of Rudolf Sturany's type specimens in the Naturhistorisches Museum Wien (NHMW): deep-sea Eastern Mediterranean molluscs. *Zoosystem Evolution*, **94** (1): 29-56.

Alf A. & Haszprunar G., 2015. *Mittelmeer Mollusken (Prosobranchia & Bivalvia). Ein Bestimmungsbuch.* ConchBooks, Hackenheim, 417 pp.

Allen J.A., 2008. Bivalvia of the deep Atlantic. *Malacologia*, **50**: 57-173.

Amano K., 1984. Two species of Mytilidae (Bivalvia) from the Miocene deposity in Hokkaido, Japan. *Venus*, **43**: 183-188.

Amano K. & Little C.T.S., 2005. Miocene whale-fall community fron Hokkaido, northern Japan. *Palaeogeography, Palaeoclimatology, Paleoecology*, **215**: 345-356.

Amano K., Little C.T.S. & Inoue K., 2007. A new Miocene whale-fall community from Japan. *Palaeogeography, Palaeoclimatology, Paleoecology*, **247**: 236-242.

Amon D.J., Coplet J.T., Dahlgren T.G., Horton T., Kemp K.M., Rogers A.D. & Glover A.G., 2016. Observations of fauna attending wood and bone deployments from two seamounts on the Southwest Indian Ridge. *Deep Sea Research, Part II Topical Studies in Oceanography.*

Ardovini R. & Cossignani T., 1999. *Atlante delle conchiglie di profondità del Mediterraneo.* L'Informatore Piceno Ed., Ancona, 112 pp.

Arduino G., Locatelli B., Orlando F. & Repetto G., 1995. *Catalogo illustrato delle conchiglie marine del Mediterraneo.* Amici del Museo "F. Eusebio", Alba, 197 pp.

Barsotti G., 1972. La ricerca delle conchiglie del Mediterraneo. II. Ordo Filibranchia (Continua). Mytilacea del Mediterraneo. *La Conchiglia*, **4**: 7-8.

Barsotti G. & Giannini F., 1974. Primo ritrovamento di *Deletopecten vitreus* (Gmelin, 1789) e nuova segnalazione di *Adula simpsoni* (Marshall, 1900) nelle acque dell'Alto Tirreno. *La Conchiglia*, **6** (64). 10,11,15.

Bernard F.R., 1978. New bivalve Mollusca, subclass Pteriomorpha, from the Northeastern Pacific. *Venus*, **37**: 61-75.

Berrow S., Nunn J., Flannery K. & Rogan F., 1995. *Adula simpsoni* (Marshall, 1900) recirded from a whake skull trawled up of South-West Ireland. *Irish Naturalists' Journal*, **25**: 150-151.

Bodwen J. & Heppel D., 1966. Revised list of British Molluska; I. Introduction; Nuculacea-Ostreacea. *Journal of Conchology*, **26**: 99-124.

Bolotin J.P., Hrs-Brenco M., Tutman P., Glavic N., Kozul V., Skaramuca B., Lucic L.J. & Dulcic J., 2005. First record of *Idas simpsoni* (Mollusca: Bivalia: Mytilidae) in the Adriatic Sea. *Journal of the Marine Biological Association of UK*, **85** (4): 977-978.

Bruschi A., Ceppodomo I., Galli C. & Piani P., 1985. *Caratterizzazione ecotipologica delle coste italiane. Catalogo dei molluschi conchiferi viventi nel Mediterraneo. Organizzazione su elaboratore elettronico.* Collana di studi ambientali, ENEA Roma, 111 pp.

Carrozza F., 1984. Microdoride di malacologia Mediterranea. *Bollettino Malacologico*, **20**: 219-226.

Chambers P. & Sowerby G., 2009. *British Seashell: A guide for Collectors and Beachcombers.* Remember When, 233 pp.

Cosel R. von & Marshall B.A., 2003. Two new species of large mussels (Bivalvia: Mytilidae) from active submarine volcanoes and a cold seep off the eastern North Island of New Zealand, with description of a new genus. *The Nautilus*, **17** (2): 31-46.

Cossignani T. & Ardovini R. (in collab. con Cecalupo A., Micali P., Tisselli M. & Cossignani V.), 2011. *Malacologia Mediterranea. Atlante delle conchiglie del Mediterraneo.* L'Informatore Piceno Ed., Ancona, 536 pp.

Cox L.R. with Nuttall C.P. & Trueman E.R., 1969. *General Features of Bivalvia.* In: Moore R.C. (ed.) – Treatise on Invertebrate Paleontology. Part N, Vol. 1 Mollusca 6 Bivalvia, pp. N3-N129.

Dall W.H., Bartsch P. & Rehder H.A., 1938. A manual of the recent and fossil marine pelecypod mollusks of the Hawaian Islands. *Bernice P. Bishop Museum Bulletin*, **153**: 1-233.

Danise S., Bertolaso L. & Dominici S., 2016. Bathymodiolinae mussel dominated Miocene whale fall from Italy. *Bollettino della Società Paleontologica Italiana*, **55** (1): 47-53.

Dautzenberg Ph., 1927. Mollusques provenant des campagnes scientifique du Prince Albert Ier de Monaco dans l'Ocean Atlantique ert dans le Golfe de Gascogne. *Resultats des Campagnes Scientifiques accomplies par Albert Ier*, **72**: 1-400.

Dell R.K., 1987. Mollusca of the Family Mytilidae (Bivalvia) associated with organic remains from deep water off New Zealand, with revision of the genera *Adipicola* Dautzenberg, 1927 and *Idasola* Iredale, 1915. *National Museum of New Zealand Records*, **3** (3): 17-36.

Dell R.K., 1995. New species and records of deep-water Mollusca from off New Zealand. *Tuhinga*, **2**: 1-26.

Duperron S., 2005. *Symbioses bactérienne de bivalves mytilidés associés aux sources de fluides en domaine océanique profond: diversuté, rôle nutritionlal et influence de l'environment.* Thèse de Doctorat, Université de Paris 6. France, 226 pp., fide Pelorce & Poitiers (2009).

Duperron S., 2010. The Diversity of Deep-Sea Mussels and Their Bacterial Symbioses. In: s. Kiel (ed.). The Vent and Seep Biota. Aspects from Microbes to Ecosystems. *Topic in Geobiology*, **33**: 137-168.

Fiala-Médioni A., 2003. *Sources of energy for deep-sea benthos in Mediterranean mud volcanoes.* Mare Incognitum? Exploring Mediterranean Deep-Sea Biology. Heraclion 2-5 Juky 2003: 77-80.

Gaudron S.M., Demoyencourt E. & Duperron S., 2012. Reproductive Traits of the Cold-Seep Symbiotic Mussel *Idas modiolaeformis*: Gametogenesis and Larval Biology. *Biological Bulletin*, **222**: 6-16.

Giannuzzi-Savelli R., Pusateri F., Palmeri A., Ebreo C. & Coppini M., Mangelli A., Bogi C., 2001. *Atlante delle conchiglie marine del Mediterraneo. Vol. 7 (BIVALVIA: Protobranchia, Pteriomorpha).* Ed. Evolver, Roma, 246 pp.

Giusti F., Mietto P. & Sbrana C., 2012. Il genere *Idas* (Mytilidae, Bathymodiolinae) in Mediterraneo, con la descrizione di quattro nuove specie. *Bollettino Malacologico*, **48**: 122-135.

Goedert J.L., Squires R.L. & Barnes L.G., 1995. Paleoecology of whale-fall habitats from deep-water Oligocene rocks, Olympic Peninsula, Washington state. *Paleogeography, Palaeoclimatology, Paleoecology*, **118**: 151-158.

Gofas S., Moreno D. & Salas C. (eds), 2011. *Moluscos marinos de Andalusia – II.* Univ. Màlaga, 343-798.

Gustafson R.G., Turner R.D., Lutz R.A. & Vrijenboek R.C., 1998. A new genus ond five new species of mussels (Bivalvia, Mytilidae) from deep sea sulfide/hydroocarbon seeps in the Golf of Mexico. *Malacologia*, **40** (1-2): 63-112.

Habe T., 1958. Descriptions of five new bivalves from Japan. *Venus*, **20**: 173-180.

Habe T., 1976. Eight new bivalves from Japan. *Venus*, **35**: 37-45.

Habe T., 1977. New and little known bivalves of Japan. *Venus*, **36**: 1-13.

Huber M., 2010. *Compendium of bivalves: A full-color guide to*

3,300 of the world's marine bivalves. A status on Bivalvia after 250 years of research. ConchBooks, Hackenheim, 901 pp. + 1CD-ROM.

I.C.Z.N., 1999. *Internazional Code of Zoological Nomenclature (Fourth edition).* The Natural History Museum. Cromwell Road, London, 306 pp.

Iredale T., 1915. Notes on the names of some British marine Mollusca. *Proceedings of the Malacological Society of London*, **11**: 329-342.

Iredale T., 1939. Mollusca, Part I. *British Museum (Natural History) Great Barrier Reef Expedition 1928-1929 Scientific Report*, **5** (6): 209-425.

Janssen A.W., 1972. Die Mollusken-Fauna der Twistringer Schichten (Miocän) von Norddeustschland. *Scripta Geologica*, **10**: 1-95.

Janssen R. & Krylova E.M., 2014. Deep-sea fauna of European seas: An annotated species ceck-list of benthic invertebrates living deeper than 2000 m in the seas bordering Europe. Bivalvia. *Invertebrate Zoology*, **11** (1): 42-82.

Jeffreys J.G., 1876. New and peculiar Mollusca of *Pecten*, *Mytilus* and *Arca* families, procured in the Valorous expedition. *Annual Magazine of natural History*, **18** (4): 424-436.

Kauffmann E.G., 1969. Form, Function, and Evolution. In: Moore R.C. (ed.). *Treatise on Invertebrate Paleontology. Part N, Vol. 1 Mollusca 6 Bivalvia*, pp. N129-N205.

Kiel S. & Goedert J.L. 2006. Deep-sea food bonanzas: early Cenozoic whae-fall communities resemble woodd-fall rather than seep comminities. *Proceedins of the Royal Society B*, **273**: 2625-2631.

Kiel S. & Goedert J.L., 2007. New mollusks associated with biogenic substrates in Cenozoic deep-water sediments of Washington state. *Acta Palaeontologica Polonica*, **52** (1): 41-52.

Koruda T., Habe T. & Koyama Y., 1981. A catalogue of molluscs of Wakayama Prefecture, the Province of Kii. *Pubblication of the Seto Marine Biological Laboratory*, sp. pubbl. **7**: 1-303.

Laming S.R., Duperron S., Cunha M.R. & Gaudron S.M., 2014. Settled, symbiotic, then sexually mature: adaptative developments, anatomy in the deep-sea, chemiosymbiotic mussel *Idas modiolaeformis. Marine Biology*, **161**: 1319-1333.

Lamy E., 1937. Revision de Mytilidae vivants du Muséum National d'Histoire Naturelle de Paris. *Journal de Conchyliologie*, **81**: 169-197.

Lorion J., Buge B., Cruaud C. & Samadi S., 2010. New insights into diversity and evolution of deep-sea Mytilide (Mollusca: Bivalvia). *Molecular Phylognesis and Evolution*, **57**: 71-83.

Lorion J., Halary S., Nascimiento J. do, Samadi S., Couloux A. & Duperron S., 2012. Evolutionary history of *Idas* sp. Med (Bivalvia: Mytilidae), a cold seep mussel bearing multiple symbionts. *Cahier de Biologie Marine*, **53**: 77-87.

Marshall J.T., 1900. On a British species of *Myrina*, with a note on the genus *Idas*. *Journal of Malacology*, **7** (7): 167-170.

Marshall J.T., 1901. Note on *Myrina simpsoni* Marsh. *Journal of Malacology*, **8** (1): 19.

Marshall J.T., 1902 – Notes on British shalls of *Buccinum*, *Fusus*, et. *Journal of Malacology*, **9** (2): 35-50.

Ministére de l'Interieur, 1875. Bibliographie de la France. *Journal général de l'imprimerie et de la libraire*, 2° s., **64** (52): 749-764.

Moore E.J., 1983. Tertiary marine pelecypods of California and Baja California: Nuculidae through Malleidae. *U.S. Geological Survey Professional Paper*, **1228-A**: 1-108.

Moore R.C. (ed.), 1969. *Treatise on Invertebrate Paleontology. Part N, Vol. 1 Mollusca 6 Bivalvia*, Geol. Soc. America & Univ. Kansas, 489 pp.

Mulsant M.A., 1875. *Catalogue Des Oiseaux-Mouches Ou Colibris.* H. Georg Libraire, Lyon; Deyrolle Naturaliste, Paris; Boucard Naturaliste, Londres, 32 pp.

Mulsant M.A., 1876. Catalogue Des Oiseaux-Mouches Ou Colibris. *Annales de la Société Linnéenne de Lyon et des Société Botanique de Lyon*, (n.s.) **22:** 199-228.

Mulsant M.A.& Verreaux E., 1876. *Histoire naturelle des oiseaux-mouches ou colibris constituant le famille des Trochilides.* Volume 3 - fascicolo 3. Publié par la Sociétè Linnéenne de Lyon, Lyon, 161-240 pp.

Nordsieck F., 1969. *Die europäischen Meeres-Gehäuseschnecken (Bivalvia) von Eismeer bis Kapverden und Mittelmeer.* G. Fischer, Stuttgart, 256 pp.

Ockelmann K.W. & Dinesen G.E., 2009. Systematic relationship of the genus *Adula* and its descent from a *Mytilus*-like ancestor (Bivalvia: Mytilidae: Mytilinae). *Steentrupia*, **30** (2):141-152.

Ockelmann K.W. & Dinesen G.E., 2011. Life on wood – the carnivorous deep-sea mussel *Idas argenteus* (Bathymodiolinae, Mytilidae, Bivalvia). *Marine Biology Research*, **7**: 71-84.

Oliver P.G. & Holmes A., 2009. *Idas lamellosus* Verrill, 1882 (Bivalvia: Mytiloidea), a woodfall mussel new to the fauna of the Northeast Atlantic. *Journal of Conchology*, **396**: 705-708.

Olu-Le-Roy K., Sibuet M., Fiala-Médioni A., Goeas S., Salas C., Mariotti A., Foucher J.-P. & Woodside J., 2004. Cold seeps communities in the deep eastern Mediterranean Sea: composition, symbiosis and spatial distribution on mud volcanoes. *Deep Sea Research, Part 1 Oceanographic Research Papers*, **51**: 1915-1936.

Oskarsson N., 1982 – *On chemical reactions in volcanic phases.* Eldur I Nordri, Societas Scientiarum Islandi, Reykjavik, pp. 275-281 (*fide* Warén, 1991).

Parenzan P., 1974. *Carta d'identità delle conchiglie del Mediterraneo. Volume secondo, Bivalvi prima parte.* Bios Taras Editrice, Taranto, 277 pp.

Pelorce J. & Poutiers J.M., 2009. Une nouvelle espèce de Bathymodiolinae (Mollusca, Bivalvia, Mytilidae) associée à des os de baleine coulés en Méditerranée. *Zoosystema*, **31** (4): 975-985.

Peters J.L., 1945. *Check-list of birds of the world.* Vol. 5, Cambridge, Harvard University Press, 306 pp.

Piani P., 1980. Catalogo dei molluschi conchiferi viventi nel Mediterraneo. *Bollettino Malacologico*, **16** (5-6): 113-224.

Poppe G.T. & Goto Y., 1993. *European Seashells. Vol. 2 (Scaphopoda, Bivalvia, Cephalopoda).* 2nd edition (2000), ConchBooks, Darmstadt, 221 pp.

Prashad B., 1932. *The Lamellibranchia of the Siboga Expedition. Systematic Part II Pelecypoda (Exclusive of the Pectinidae).* E.J. Brill, London, 353 pp.

Quero J.-C., 1973. Présence d'*Adula simpsoni* sur un crâne de *Globicephala melaena* ramassé au chalut au Golfe de Gascogne. *Annales de la Société des Sciences Naturelles de Charente-Maritime*, **5**: 319-320.

Repetto G., Orlando F. & Arduino G., 2005. *Conchiglie del Mediterraneo.* Amici del Museo "Federico Eusebio", Alba, 392 pp.

Ritt B., Duperron S., Lorion S., Lazar C.S. & Sarrazin J., 2012. Integrative study of a new cold-seep mussel (Mollusca: Bivalvia) associated with chemosinthetic symbionts in the Marmara Sea. *Deep Sea Research*, **67**: 121-132.

Rodrigues C.F., Laming S.R., Gaudrn S.M., Oliver G., Le Bris N. & Duperron S., 2015. A sad tale: has the small mussel *Idas argenteus* lost its symbionts? *Biological Journal of the Linnean Society*, **114**: 398-405.

Sabelli B., Giannuzzi-Savelli R. & Bedulli D., 1990. *Catalo-*

go annotato dei molluschi marini del Mediterraneo – Annotated ceck-list of Mediterranean marine mollusks. Ed. Libreria Naturalistica Bolognese, Bologna, 348 pp.

Saether K.P., Little C.T.S., Campbell K.A., Marshall B.A., Collins M. & Alfaro A.C., 2010. New fossil mussels (Bivalvia: Mytilidae) from Miocene hydrocarbon seep deposits, North Island, New Zealand, with general remarks on vent and seep mussels. *Zootaxa*, **2577:** 1-45.

Salas C., 1996. Marine Bivalves from off the Southern Iberian Peninsula collected by the Balgim and Fauna 1 expedition. *Haliotis*, **25**: 33-100.

Samadi S., 2014. Campagnes des deuxième gémération: la faune des bois coulés. Second generation cruises: the sunken woods fauna. *Xenophora*, **126**: 52-53.

Signorelli J.H. & Crespo E., 2017. First record of the genus *Adipicola* (Mollusca Bivalvia: Mytilidae) and description of a new species from the Argentine SW Atlantic Ocean. *Zootaxa*, **4813** (2): 325-338.

Smith C.R. & Baco A.R., 2003. Ecology of whale falls and deep-sea floor. *Oceanography and Martine Biology. An Annual Review*, **41**: 311-354.

Smith E.A., 1885. Report on the Lamellibranchiata collected during the voyage of H.M.S. "Challenger". *Challenger Report, Zoology*, **13**: 1-341.

Smith E.A., 1904. Natural history notes from H. M. Indian Marine Survey Streamer *"Investigator"*. – Ser. 3, No. 1, On Mollusca from the Bay of Bengal and the Arabian Sea. *Annals and Magazine of Natural History*, **14** (7): 1-14.

Soot-Ryen T., 1955. A report on the family Mytilidae (Pelecypoda). *Allan Hancock Pacific Expeditions*, **20** (1): 1-175.

Southward E.C., 2008. The morphology of bacterial symbioses in the gills of mussels of the genera *Adipicola* and *Idas* (Bivalvia: Mytilidae). *Journal of Shellfish Research*, **27**: 1-623.

Southward E.C., Andersen A.C. & Hourdez S., 2011. *Lamellibranchia aximandri* n. sp., a new vestimentiferan tubeworm (Anellida) from the Mediterranean, with notes on frenulate tubewoms from the same habitat. *Zoosystema*, **33** (3): 245-279.

Sturany R., 1896. Zoologische Ergbnisse VIII. Mollusken I (Prosobranchier und Opistobranchier; Scaphopoden; Lamellibranchiaten) gesammelt von S.M. Schift "Pola" 1890-1894. *Denkschriften der mathematisch-naturwissenschaftlichen Klasse der kaiserlichen Akademie der Wissenschaften*, **63**: 1-36.

Taviani M., 2011. The deep-sea chemoautotroph microbial world as experienced by Mediterranean metazoans trough time. In: Reitner J., Quéric N.-V. & Arp G. (eds). *Advances in stromatolite geobiology. Lecture Notes in Earth Sciences*, Berlin, **131**: 277-295.

Taylor J.D. & Glover E.A., 2010. Chemiosymbiotis bivalves. In: Kiel S. (ed.). *The vent and seep biota: aspects from microbes to ecosystems*. Springer: 107-136.

Tebble N., 1966. *British Bivalve Seashells*. Royal Scottish Museum, Edimbourg, 2nd edition (1976), 212 pp.

Terreni C., 1981. *Molluschi conchiferi del mare antistante la costa toscana (Gastropoda, Scaphopoda, Amphineur, Bivalvia, Cephalopoda)*. Tip. Benvenuti & Cavaciocchi, Livorno, 106 pp.

Thiele J. & Jaeckel S., 1932. Muscheln der Deutschen Tiefsee-Expedition. *Wissenschaftlichen Ergebnisse der Deutschen Tiefsee-Expedition*, **21**: 161-268.

Tunncliffe V., McArthur A.G. & MccHugh D., 1998. A Biogeographical Perspective of the Deep-Sea Hydrotermal Vent Fauna. *Advance in Marine Biology*, **34**: 355-442.

Van Regteren Altena C.O., 1964. *Idasola argentea* (Jeffreys) washed ashore on the Dutch coast. *Basteria*, **28** (5): 83-85.

Verco J.C., 1908). Notes on South Australia marine Mollusca, with description of new species – Part IX. *Transactions of the Royal Society od South Australia*, **32**: 338-361.

Verrill A.E., 1882. Catalogue of marine Mollusca added to the fauna of the New England region, during the last ten years. *Transactions of the Connecticut Academy od Arts and Sciences*, **5** (2): 447-587.

Vieillot L.J.P., 1817. Colibri. In *Nouveau dictionnaire d'histoire naturelle, appliquée aux arts, a l'agriculture, a l'économie rurale et domestique, à la médicine, etc.* Vol. 7. A. Lanoe, Paris, 340-376 pp.

Vokes H.E., 1967. Genera of the Bivalvia: A systematic and bibliographic catalogue. *Bulletin of American Paleontology*, **51** (232): 103-394.

Warén A., 1980. Marine Mollusca described by John Gwyn Jeffreys, wth the loation of the type material. *Conchigliological Society of Great Britain & Ireland*, sp. pubbl., **1**: 1-60.

Warén A., 1991. New and little known Mollusca from Iceland and Scandinavia. *Sarsia*, **76**: 53-124.

Warén A., 1993. New and little known Mollusca from Iceland and Scandinavia. Part 2. *Sarsia*, **78**: 159-201.

Warén A. & Carrozza F., 1990. *Idas ghisottii* sp. n., a new Mytilid bivalve associated with sunken wood in the Mediterranean. *Bollettino Malacologico*, **26** (1-4): 19-24.

Woodward S.P., 1854. *A manual of the Mollusca; or rudimentary treatise of recent and fossil shells*. Part 2. John Weale, London, xii + 159-330 pp.

Woodward S.P., 1856. *A manual of the Mollusca; or rudimentary treatise of recent and fossil shells*. Part 3. John Weale, London, 331-486 pp.

Yonge C.M., 1978. Significance of the ligament in the classification of the Bivalvia. *Proc. R. Soc. London*, B 202: 231-248.

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An abyssal-ultraabyssal chiton (Mollusca: Polyplacophora) with a wide distribution

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Abstract

The world deepest polyplacophoran species, the wood-associated *Leptochiton vitjazae* (Sirenko, 1977) is re-studied based on additional material that allowed a better understanding of the species' characteristics and distribution. It is shown that the species occurs in both emisferes within the western Pacific trench system and with a wider bathymetrical range than previously known. A combined set of morphological characteristics allowed a grouping of similar constituted Pacific congeners within the *Leptochiton vitjazae*-group. Species which fall into this group share, besides their deep-water habitat, also a similar feeding type, very short gill rows (4 gills), low number of radula teeth rows, and a tricuspidate head of the second lateral tooth. A limited genetic analysis mainly based on a mitochondrial cytochrome c oxidase I (COI) sequence helped to attribute a recently unnamed species record from another ultraabyssal region to the same group.

Key words

Lepidopleuridae, Pacific Ocean, distribution, bathymetry, specific characters

Riassunto

Leptochiton vitjazae (Sirenko, 1977), la specie di poliplacoforo più profonda viene riesaminata attraverso ulteriore materiale che ha permesso una migliore comprensione delle caratteristiche e della distribuzione della stessa. Viene dimostrato che la specie ha una distribuzione che interessa i due emisferi nel sistema di fosse del Pacifico con una escursione batimeterica più ampia di quanto noto. Un set combinato di caratteristiche morfologiche ha consentito di raggruppare simili congeneri del Pacifico nell'ambito del gruppo del *Leptochiton vitjazae*. Le specie che ricadono in questo gruppo condividono oltre all'habitat di profondità anche un medesimo tipo di alimentazione, serie molto corte di branchie (4 branchie), un basso numero di file di denti della radula e un secondo laterale tricuspidato. Un'analisi genetica limitata basata essenzialmente sulla sequenza della citocromo c ossidasi I mitocondriale (COI) ha aiutato nell'attribuire al medesimo gruppo esemplari non identificati ritrovati recentemente in un'altra regione ultraabissale.

Parole chiave

Lepidopleuridae, Oceano Pacifico, distribuzione, batimetria, caratteri specifici.

Introduction

Deep-sea species of the molluscan class Polyplacophora are scarce and their diversity is not comparable to their representatives of the shelf's photic zone. In the most recent compilation covering the polyplacophorans found below 2000 m, Schwabe (2008) listed six species of the genus *Ferreiraella* Sirenko, 1988, 14 species of the genus *Leptochiton* Gray, 1847, three species of the genus *Stenosemus* von Middendorff, 1847 and a single species of the genus *Lepidozona* Pilsbry, 1892. According to this list, there are only two described species of chitons living in the ultra-abyssal zone deeper 6000 m (following Menzies & George, 1967), namely *Ferreiraella caribbensis* Sirenko, 1988 (Caiman Trench, 6740-6780 m), and *Leptochiton vitjazae* (Sirenko, 1977) (Bougainville Trench, 6920-7657 m). Unfortunately, Schwabe (2008) missed two earlier lepidopleurid records from the ultra-abyss of the New Hebrides Trench (Belyaev, 1966) and from Palau (Belyaev & Mironov, 1977) and additionally Wang et al. (2018) provided a new record of a *Leptochiton* from the Yap Trench. These data show that the members of the order Lepidopleurida mainly contribute to the polyplacophoran deep-sea fauna. This is even true for shallower deep water zones. From about 160 species of polyplacophorans inhabiting depths below 200 m, 70% belong to Lepidopleurida (Sirenko, 1997 with additional own data). Noteworthy, of 170 recent species of this order 61% are from deep water and 20% of them cross the border of 1000 m.

Aim of the present study is the re-description of *Leptochiton vitjazae* (Sirenko, 1977) based on newly available material to allow a better morphological and biogeographical understanding of the world's deepest polyplacophoran species.

Material and methods

We used historic *Leptochiton* samples, collected during the cruises 22, 26 and 57 of the Russian research vessels *Dmitry Mendeleev* in 1975 and *Vitjaz* in 1955, 1959 and 1975 (at Zoological Institute, Russian Academy of Sciences, St. Petersburg, here after ZISP) and also a new sample, which was collected during the KuramBio expedition with the German research vessel *Sonne* in 2012

(at Bavarian State Collection of Zoology, München, Germany, here after ZSM). All examined samples contained pieces of sunken wood.

Specimens selected for a scanning electron microscopy (SEM) study were treated following Sirenko (2015). Several valves (usually valves I, IV, V and VIII), an anterior portion of the radula and a portion of the girdle were chosen for a Scanning Electron Microscope FEI SEM Quanta 250 scan. The remains of the radula and girdle were dried and embedded in Canada balsam for examination with a light microscope. SEM features of studied specimens are presented in detail. Bathymetric ranges are reported as values between the shallowest and deepest stations as explained by Bouchet et al. (2008). The systematics follows Sirenko (2006) with slight alterations.

On our request the molecular work was done by *Advanced Identification Methods - AIM* GmbH (Munich, Germany), following exactly the methods of Wang et al. (2018). For this purpose we provided piece of the foot of the smaller specimen of the Kurambio sample deposited in the ZSM (ZSM Mol 20130026, body length: BL 11.5 mm). Although we have both mitochondrial cytochrome c oxidase I (COI) gene and nuclear 28S ribosomal RNA gene (28S rDNA), only the COI sequence were analyzed to test the phylogenetic relationship among our specimen and the taxa Wang et al. (2018, tab. 1) used. For the alignment we renamed their taxon names "*Leptochiton* n. sp. 4" to "*Leptochiton samadiae* Sigwart & Sirenko, 2012" (following Sigwart & Sirenko, 2012), as well as "*Leptochiton* sp. 1" and "*Leptochiton* sp. s" to "*Leptochiton* sp. (Yap larger)" and "*Leptochiton* sp. (Yap smaller)", respectively. Further, we had to use the function "reverse complement" for both, "*Leptochiton* sp. 1" and "*Leptochiton* sp. s", while aligning. Sequence data of *Leptochiton vitjazae* (ZSM Mol 20130026), are uploaded in BOLD (http://www.boldsystems.org/) under the dataset: DS-ESLEPTOV (dx.doi.org/10.5883/DS-ESLEPTOV), with the process ID: AIMEI015-19, and are also transferred to GenBank (https://www.ncbi.nlm.nih.gov/genbank/), under the accession numbers „MN135743" for COI and „MN135754" for the 28S sequences.

Taxonomy

Class Polyplacophora Gray, 1821
Subclass Neoloricata Bergenhayn, 1955
Order Lepidopleurida Thiele, 1909
Family Leptochitonidae Dall, 1889
Genus *Leptochiton* Gray, 1847

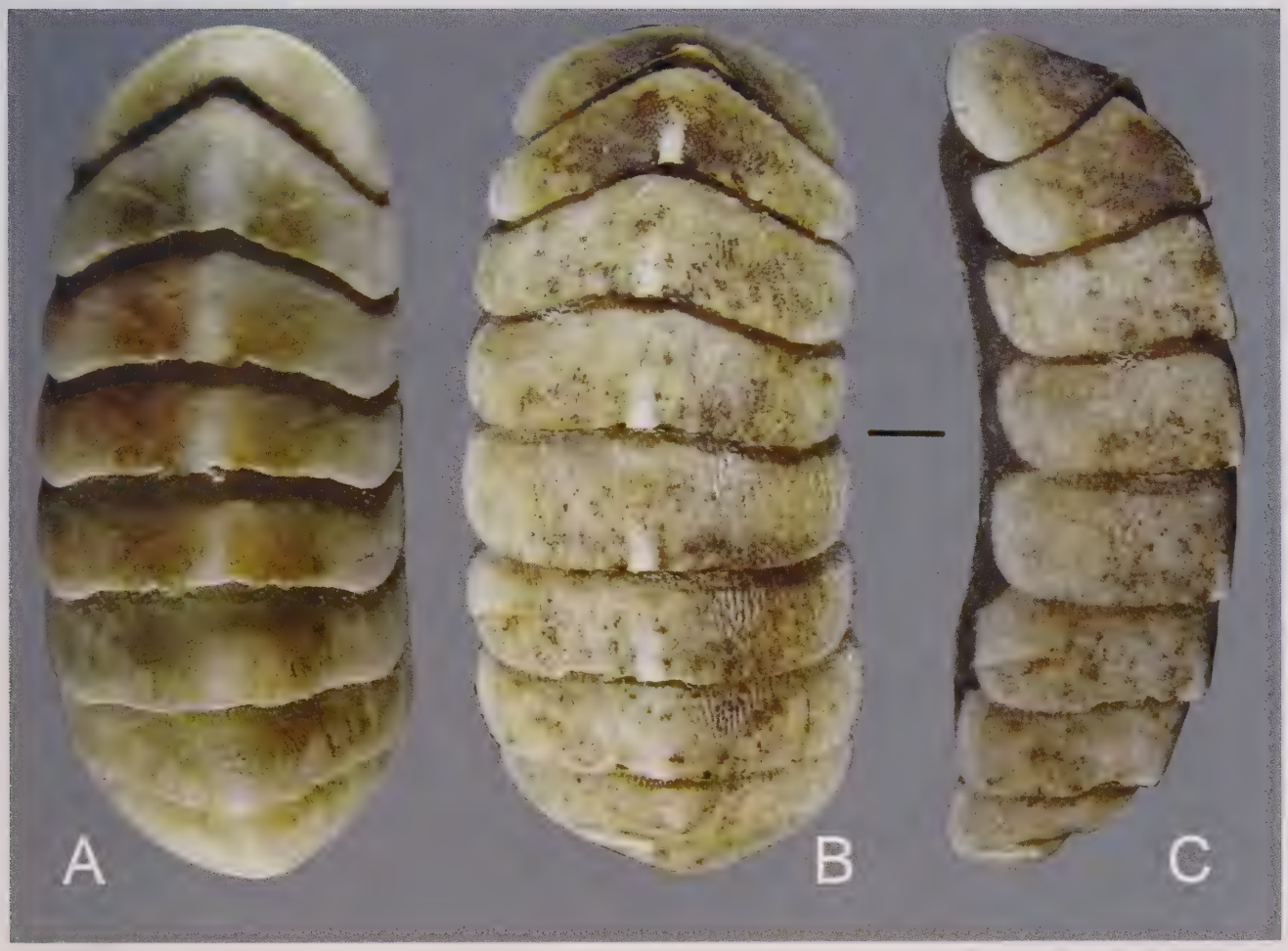

Fig. 1. Complete specimens of *Leptochiton vitjazae*, paratype (ZISP 1857), BL 13.0 mm, (**A**); and specimen (ZISP 2307), BL 14.5 mm (**B**, **C**). **A**, **B**. Dorsal view; **C**. Lateral view.

Fig. 1. Esemplare completo di *Leptochiton vitjazae*, paratipo (ZISP 1857), BL 13,0 mm, (**A**); e esemplare (ZISP 2307), BL 14,5 mm (**B**, **C**). **A**, **B**. Vista dorsale; **C**. Vista laterale.

Type species. *Chiton cinereus*; Montagu 1803 (non *Chiton cinereus* Linnaeus, 1767) = *Leptochiton asellus* (Gmelin, 1791) fide Lovén (1846), subsequent designation by Gray (1847).
Genus distribution. Worldwide, Carboniferous – Recent.

Leptochiton vitjazae (Sirenko, 1977)
(Figs 1-8)

Lepidopleurus sp.; Belyaev 1966: 105; Belyaev & Mironov 1977: 13, 21, pl. 1-fig. 9.

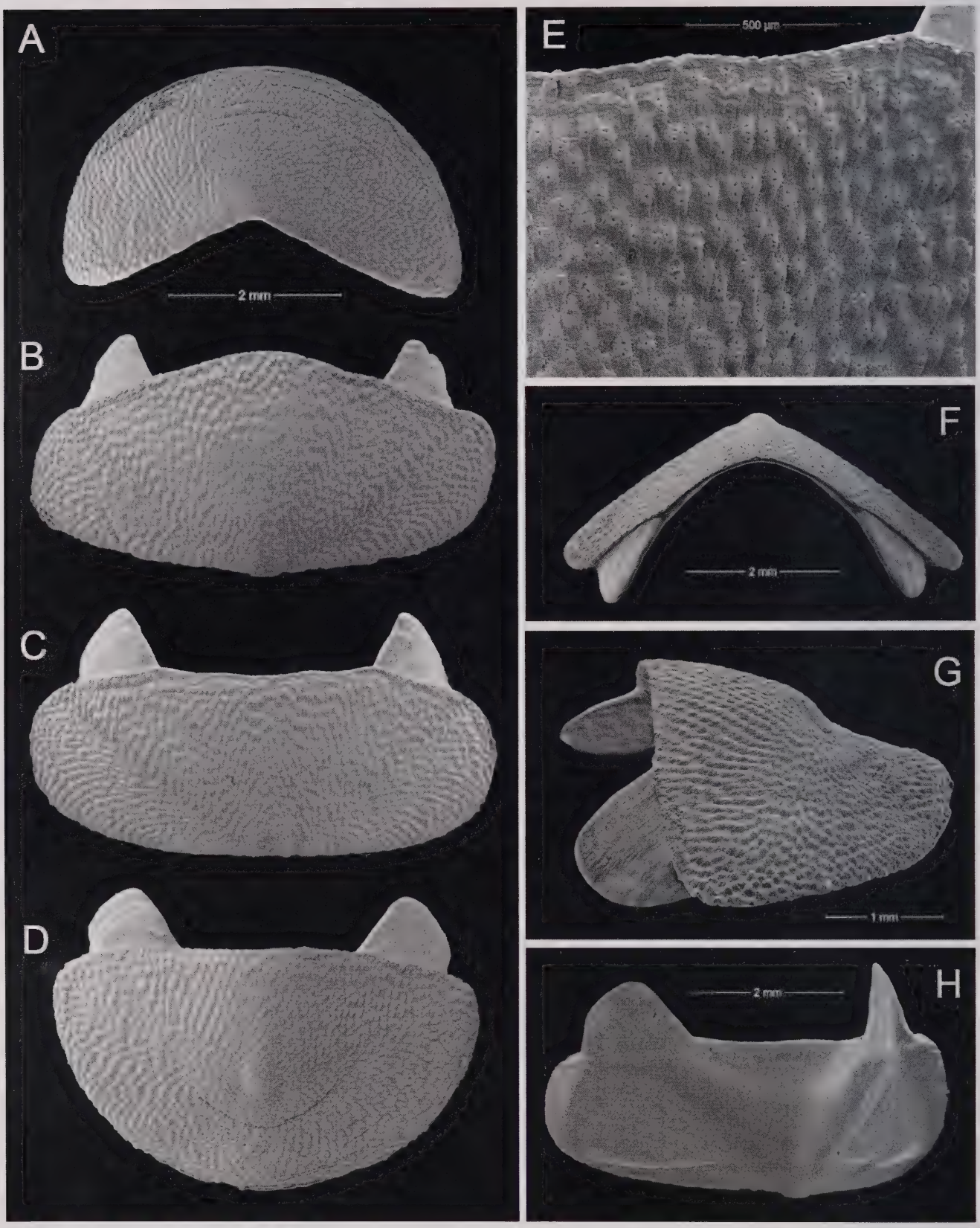

Fig. 2. *Leptochiton vitjazae* specimen (ZISP 2307), BL 14.5 mm. **A**. Valve I, dorsal view; **B**. Valve II, dorsal view; **C**. Valve V, dorsal view; **D**. Valve VIII, dorsal view; **E**. Valve V, tegmentum sculpture in central and lateral areas; **F**. Valve V, rostral view; **G**. Valve VIII, lateral view; **H**. Valve VI, ventral view.

Fig. 2. *Leptochiton vitjazae* esemplare (ZISP 2307), BL 14,5 mm. **A**. Valva I, vista dorsale; **B**. Valva II, vista dorsale; **C**. Valva V, vista dorsale; **D**. Valva VIII, vista dorsale; **E**. Valva V, scultura del tegmentum nelle zone centrale e laterale; **F**. Valva V, vista rostrale; **G**. Valve VIII, vista laterale; **H**. Valva VI, vista ventrale.

Leptochiton sp. (partim); Belyaev 1989: 84.
Lepidopleurus vitjazi Sirenko 1977: 1108, figs 1-13; 1988: 1781; Ferreira 1980: 59; 1981: 328.
Leptochiton vitjazi; Kaas & Van Belle 1980: 142; Belyaev 1989: 84; Kaas et al. 1998: 165; Sirenko 1998: 5; 2001: 53, 55, 57; 2004: 112, 114, 115; 2015: 152, 154, 198; Sigwart & Sirenko 2012: 7, 8, 23.
Lepidopleuris vitjazi; Belyaev 1983: 290.

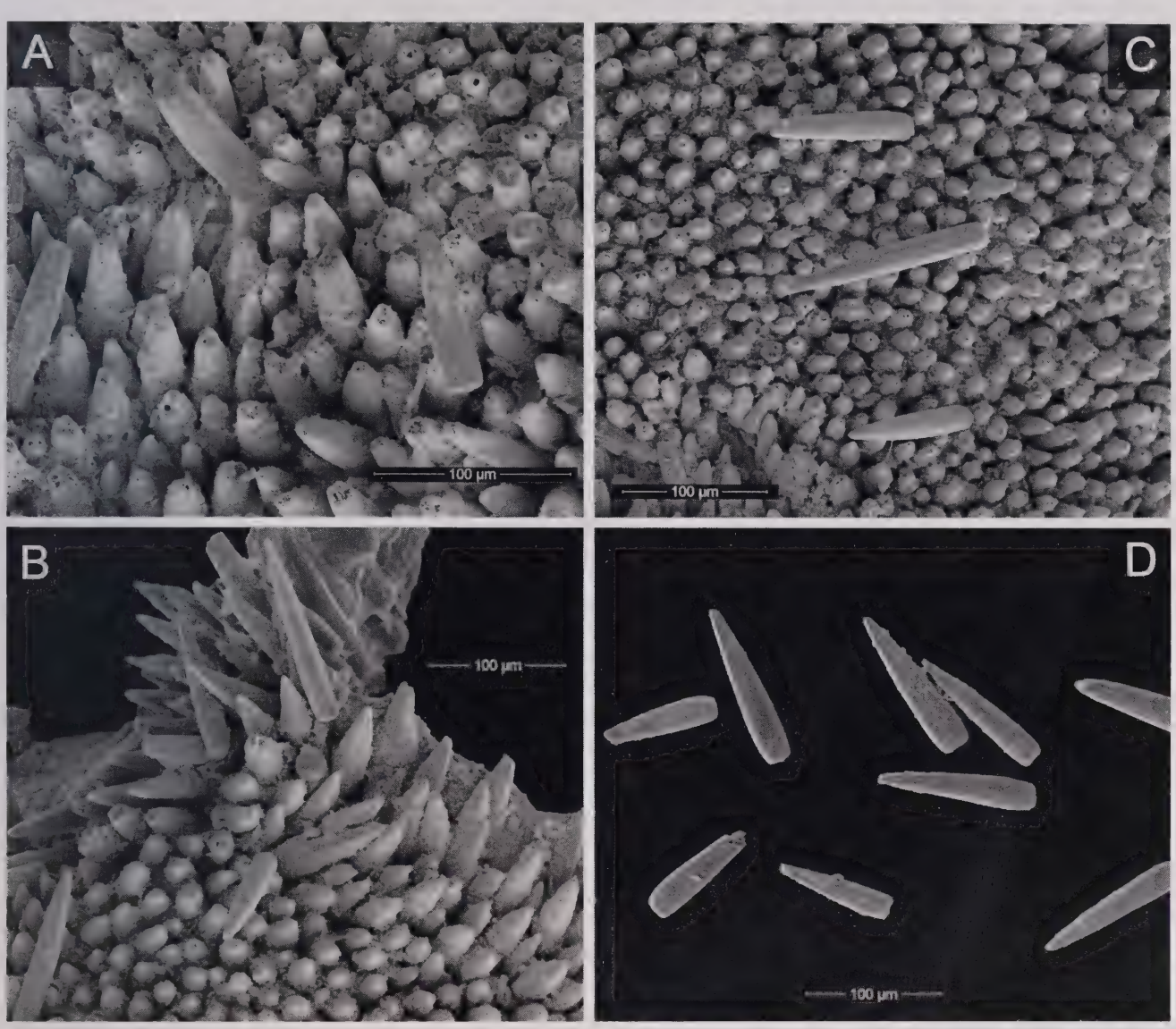

Fig. 3. *Leptochiton vitjazae*, specimen (ZISP 2307), BL 14.5 mm. **A-D**. Dorsal, marginal and ventral spicules; **C**. Sutural scales and needles.

Fig. 3. *Leptochiton vitjazae*, esemplare (ZISP 2307), BL 14,5 mm. **A-D**. Spicole dorsali, marginali e ventrali; **C**. Scales ed aghi suturali.

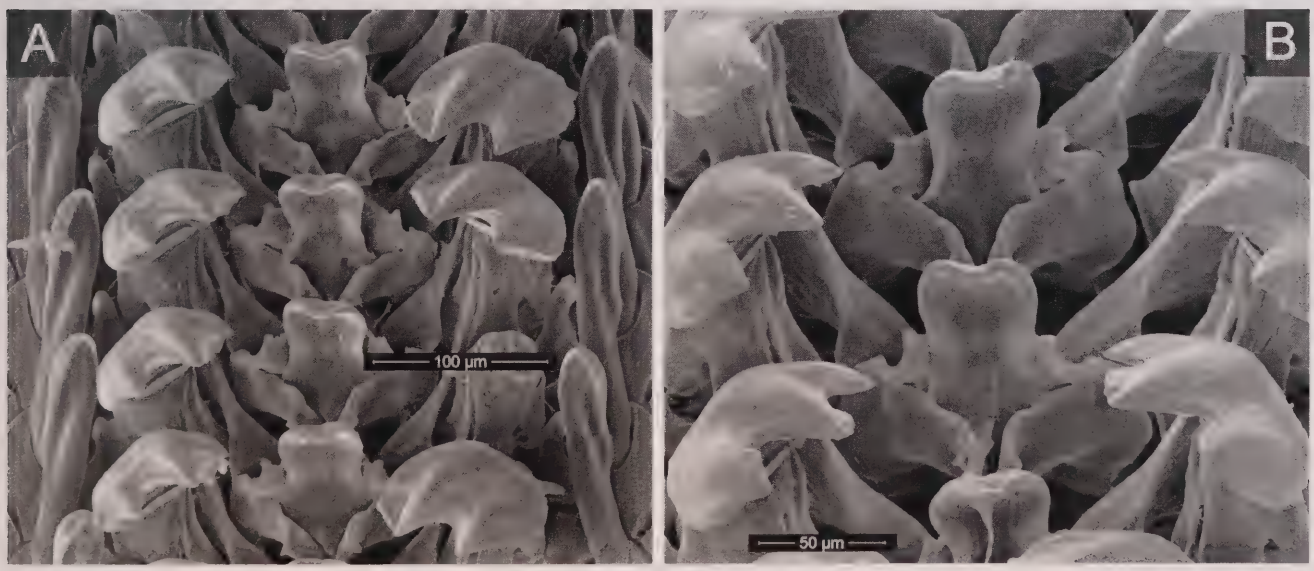

Fig. 4. *Leptochiton vitjazae* esemplare (ZISP 2307), BL 14.5 mm. **A**. Radula; **B**. Central, first lateral and major lateral teeth of radula.

Fig. 4. *Leptochiton vitjazae* esemplare (ZISP 2307), BL 14,5 mm. **A**. Radula; **B**. Denti centrali, primo laterale e maggiori laterali della radula.

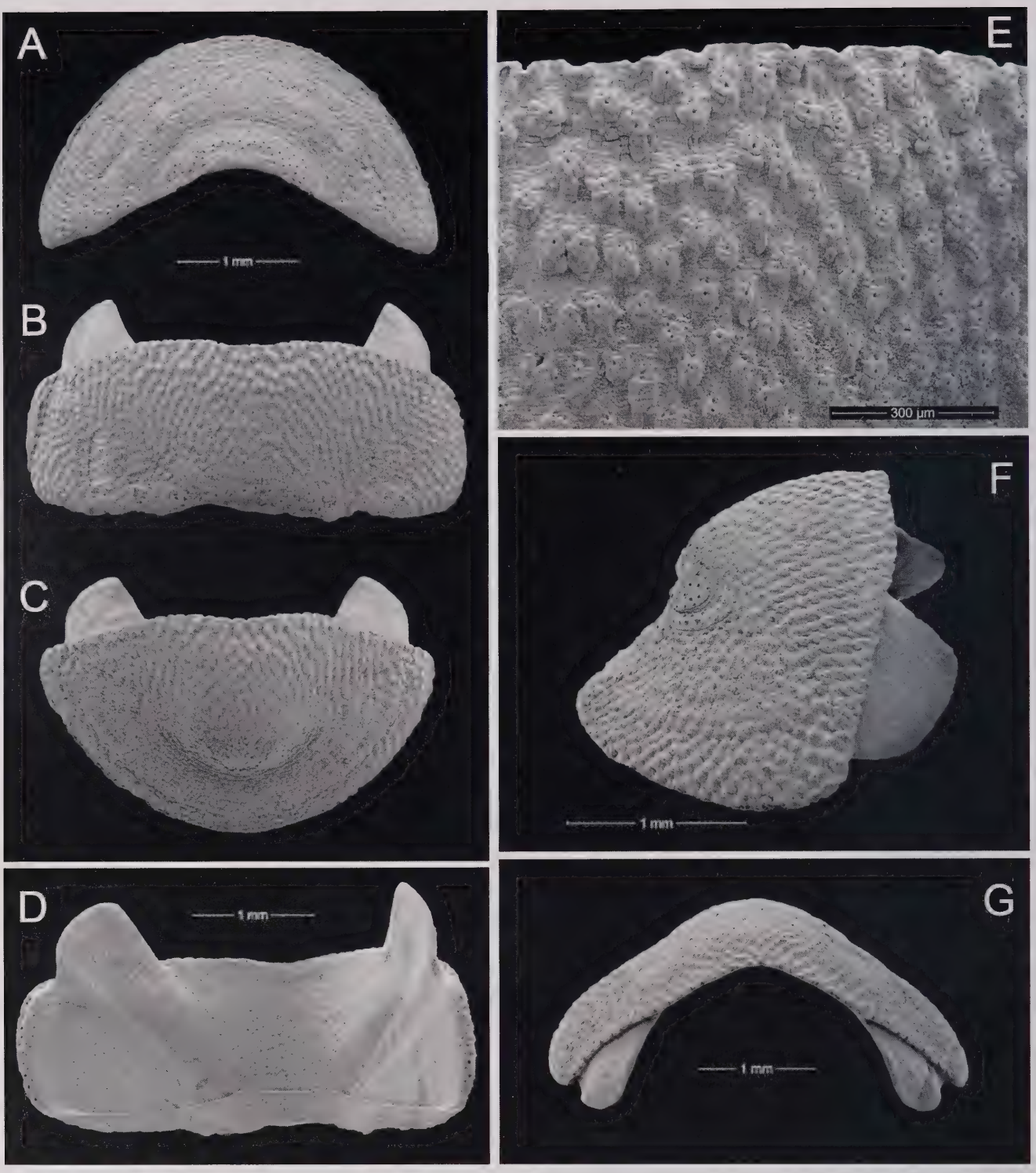

Fig. 5. *Leptochiton vitjazae*, specimen (ZISP 2308), BL 8.3 mm. **A**. Valve I, dorsal view; **B**. Valve V, dorsal view; **C**. Valve VIII, dorsal view; **D**. Valve VI, ventral view; **E**. Valve V, tegmentum sculpture in central and lateral areas; **F**. Valve VIII, lateral view; **G**. Valve V, rostral view.

Fig. 5. *Leptochiton vitjazae*, esemplare (ZISP 2308), BL 8,3 mm. **A**. Valva I, vista dorsale; **B**. Valva V, vista dorsale; **C**. Valva VIII, vista dorsale; **D**. Valva VI, vista ventrale; **E**. Valva V, scultura del tegmentum nelle zone centrale e laterale; **F**. Valva VIII, vista laterale; **G**. Valva V, vista rostrale.

Leptochiton (*Leptochiton*) *vitjazi*; Kaas & Van Belle; 1985: 120, fig. 53, map 43.

Leptochiton vitjazae; Kaas & Van Belle 1998: 200; Schwabe 2008: 215; Jamieson 2015: 155, 305.

Leptochiton cf. *assimilis* (non *Leptochiton assimilis* Thiele, 1909); Schwabe et al. 2015: 379, 385, figs 1C, 3D.

"Chitonophilidae" (partim); Jamieson 2015: 150 (a copepod term obviously misused for Leptochitonidae, depth and subsequent species citation indicate that this term in part refers to the present species)

Leptochiton vitjasi; Sirenko 2016: 62.

? *Leptochiton* sp.; Wang et al. 2018: 206, fig. 1.

Type material

Holotype (ZISP 1856).

Type locality

RV *Vityaz* cruise 25, sta. 3655, 5°49′4″S, 152°53′4″E, Solomon Sea, Bougainville Trench, 6920-7657 m.

Material examined

Solomon Sea, Bougainville Trench, RV *Vityaz* cruise 25, sta. 3655, 5°49′4″S, 152°53′4″E, 6920-7657 m. holotype (ZISP 1856), BL 11.0 mm and two paratypes (ZISP 1857), BL 12.0-14 mm, 20.07.1957; Philippine Sea, Kikai Basin, RV *Vityaz*, cruise 22, stn 3535, 28°50′6″N, 131°55′2″E, 5620-5610 m, 1 spm, BL 18.5 mm, 31.10.1955; Palau Trench, RV *Vityaz*, cruise 57, stn 7291, 7°52′N, 135°2′E, 7000-7170 m, 1 spm, BL 11.0 mm, 27.03.1975; Bismarck Sea, Manus Trench, RV *Vityaz*, cruise 57, stn 7325, 1°51′S, 144°40′E, 2580-2250 m, 1 spm (ZISP 2308), BL 8.3 mm, 10.04.1975; Solomon Sea, New Britain Trench, RV *Dmitry Mendeleev*, cruise 16, stn 1234, 7°31′1″S, 149°51′1″E, 5200 m, 1 spm (ZISP 2309), BL 13.5 mm, 15.12.1975; Abyssal northwest Pacific Plaine east of the Kuril-Kamchatka Trench, KuramBio, RV *Sonne*, AGT stn 10-11, 41°12.04′N, 150°5.87′E-41°10.78′N, 150°6.34′E, 5257-5236 m, 1 spm, BL 14.5 mm, 27.08.2012 (ZISP 2307), 2 spms BL 11.5-13.8 mm (ZSM Mol 20130026).

Distribution (Fig. 7)

The species is yet only confirmed from the above listed material, and ranges bathymetrically between 2580-7000 m.

Extended description

Animal elongate oval, small to medium sized, BL up to 18.5 mm. Valves solid, subcarinated, highly elevated (elevation ratio 0.55-0.57 in valve V), not beaked but apex is clearly separated by lateral depressions. Color of tegmentum white.

Head valve semicircular, equal to tail valve or sometimes little wider or narrower than last valve. Intermediate valves rectangular, side margins rounded, lateral areas not raised, but diagonal line distinguishable, anterior margin convex in valve II and almost straight in other intermediate valves, posterior margin straight, not beaked. Length of tail valve shorter than half the width, mucro behind the middle, antemucronal slope weekly convex, postmucronal slope concave.

Tegmentum uniformly sculptured with oval granules arranged in a random manner, partly much crowded, especially in lateral areas forming short, curved series, in other places more or less regularly disposed, each

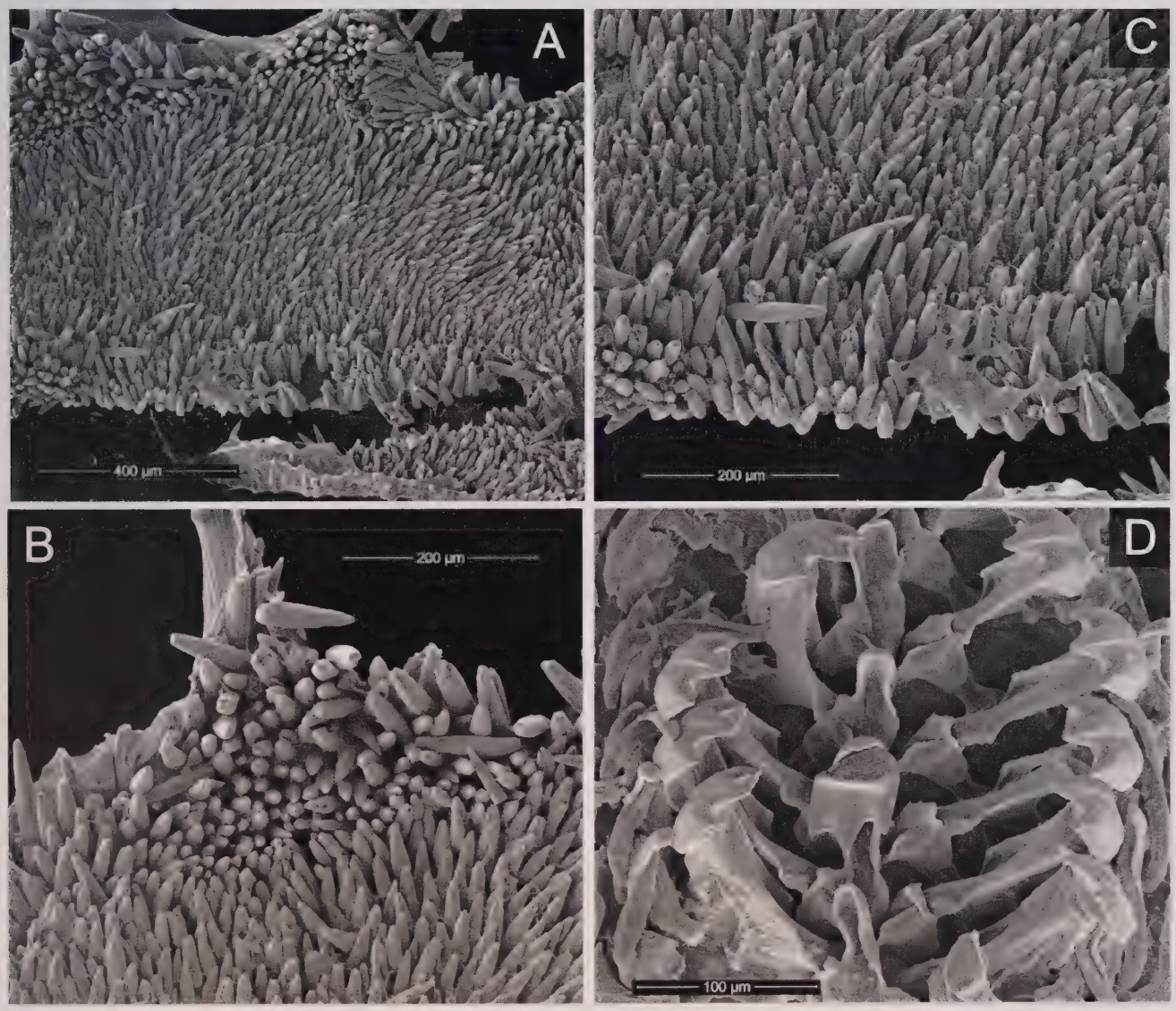

Fig. 6. *Leptochiton vitjazae*, specimen (ZISP 2308), BL 8.3 mm. **A**, **C**. Dorsal, marginal and ventral spicules; **B**. Sutural spicules and needles; **D**. Radula.

Fig. 6. *Leptochiton vitjazae*, esemplare (ZISP 2308), BL 8,3 mm. **A**, **C**. Spicole dorsali, marginali e ventrali; **B**. Spicole suturali ed aghi; **D**. Radula.

Fig. 7. Map of distribution of *Leptochiton vitjazae* with major surface currents. Circles refer to the examined material the square refers to the *Leptochiton* record of Wang et al. (2018) from the Yap trench.

Fig. 7. Mappa della distribuzione di *Leptochiton vitjazae* con le correnti maggiori di superficie. I circoli indicano il materiale esaminato, i quadrati i ritrovamenti di *Leptochiton* di Wang et al. (2018) dallo Yap trench.

granule with two or three pores of aesthetes often arranged in a single line, all aesthete pores of approximately equal size.

Articulamentum well developed, apophyses narrow, triangular with rounded top, in the intermediate valves, trapezoid in tail valve. Jugal sinus wide.

Girdle very narrow (about 0.3 mm near valve V), dorsally covered with spicules and needles. Spicules elongate, sharply pointed in the middle of the girdle (85 x 26 µm), near the valves up to 115 µm. Needles, 100-215 µm long, chiefly at the sutures, sparsely on the rest of the girdle. The marginal needles are alike. Ventrally, girdle

covered with elongate smooth spicules (up to 60 x 14 µm).
Radula of 14.5 mm long specimen (ZISP 2307), 5.1 mm long, with 36 transverse rows of mature teeth. In an 8.3 mm long specimen, radula of specimen 3.5 mm long, with 37 transverse rows of mature teeth. Central tooth rather wide, rectangular with slight constriction at central shaft, blade slightly bent downwards, distally with shallow depression, first lateral short, S-shaped, covering the lower half of central tooth, posterior margin serrated, head of major lateral tooth with three sharp denticles, the central one largest, first uncinal tooth considerable long, distally thickened, more or less hook-like, third uncinal slender and spoon-shaped.
All studied specimens have four rather short gills per side arranged from valve VII to anus, gills c. 400 µm long and wide, each with 9-10 lamellae.

Remarks

Leptochiton vitjazae is similar to *L. vanbellei* Sirenko, 2001, *L. thandari* Sirenko, 2001, *L. deforgesi* Sirenko, 2001 and *L. luridus* (Dall, 1902). It differs from them by having the granules arranged in a random manner (vs. granules arranged quincuncially), the oval granules with two or three pores of aesthetes often arranged in a single line (three pores and not arranged in a single line in *L. vanbellei*, five pores in *L. thandari* and *L. deforgesi*), shorter gill filaments and antemucronal area proportional longer than postmucronal area. Superficially, *L. vitjazae* also resembles *L. consimilis* Sigwart & Sirenko, 2012 but differs from the latter by having four short gills (vs. 45 rather long gills in *L. consimilis*), 2-3 aesthetes per granule (vs. 5 aesthetes in *L. consimilis*).

The sequences of our material were blasted on GeneBank resulting in a 100% match for the 28S for the Wang et al. (2018) Yap specimen "*Leptochiton* sp_s" while their larger specimen "*Leptochiton* sp._l" fitted to 99.82%. Our 641 base pair long COI sequence corresponded to 98.75% and 98.91%, respectively. A direct comparison between our COI sequence and "*Leptochiton* sp._l" showed seven variable sites and a p distance of 0.011, while the p distance was 0.013 to "*Leptochiton* sp_s" with eight polymorphisms. Adding the same taxon sampling and the new material Wang et al. (2018) cited, we reconstructed a Neighbour-joining tree of which we here only show the resulting subtree that contained the Yap specimens (**Fig. 8**) as the whole tree shows similar low support as in Wang et al. (2018) and require more data for an analysis of the phylogenetic position of this clade within the Lepidopleurida. The well supported clade shows that *Leptochiton vitjazae* is sister to the both specimens from the Yap trench, forming together a sister group to *L. boucheti* Sirenko, 2001, *L. vanbellei*, and *L. deforgesi*. All these taxa form together with *L. samadiae* a clade which we partly morphological consider belonging to the *L. vitjazae* group (see below).
Despite slight genetic divergences of the comparable sampling size, we tentatively place the new *Leptochiton* record of Wang et al. (2018) from the northern Yap Trench (9.8675°N, 138.5156°E, 6754 m) in the present species concept due to the overwhelming morphological similarities, although some slight differences occur. The latter (e.g. lower elevation, straighter postmucronal slope) may interpreted as intraspecific variation, but it should be noted that the authors obviously got their measurements from intact not disarticulated specimens. Further support comes from the geographic and bathymetric range, which lies within the present species concept.

Discussion

As Sigwart et al. (2011) demonstrated, the genus *Leptochiton* cannot regarded as monophyletic. Due to the sometimes limited original descriptions, the character's plasticity, and the difficulties to gain fresh material, especially of the majority of taxa from deep-sea environments, the current genus concept is in a wider sense applied. Sirenko (2004), while examination of plant remains associated polyplacophorans, discerned morphological similarities within several members of deep-sea leptochitonds. He established species-groups with similar morphologies and subsequent works by him (see references) added several more groups, which might help untangling the genus-concept. Among these species groups Sirenko (2004) established was also the *L. vitjazae* group, which at this time comprised: *L. vanbellei*, *L. thandari*, and *L. deforgesi*, besides the name bearer.
Meanwhile several new taxa were described and the restudy of some type material (by BS) allows a better understanding of this group. Neither the arrangement and distinctness of the tegmental granulation, nor the main dorsal girdle elements seem stable enough to define the group. The combination of radular and gill characters is probably more meaningful. So we define here apparently adult, medium sized, deep-water leptochitonids with a tricuspidated head of the major lateral tooth, a low number of mature teeth rows (≤ 40), and with 4 gills to the *L. vitjazae* group. The group comprises now: *L. vitjazae*, *L. boucheti*, *L. deforgesi*, *L. dykei* Sigwart & Sirenko, 2012, *L. kantori* Sirenko, 2016, *L. longisetosus* Sigwart & Sirenko, 2012, *L. rogeri* Sigwart & Sirenko, 2015, *L. samadiae* Sigwart & Sirenko, 2012, *L. schwabei* Sigwart & Sirenko, 2012, *L. thandari*, *L. vanbellei*, *L. vanuatuensis* Sirenko, 2016, and *L. wui* Sirenko, 2018. All these species inhabit the western Pacific Ocean and feed on plant remains. Additionally, they usually do not have elevated lateral areas and protruding apices (both slightly indicated in *L. vanuatuensis*), but show lateral apical depressions (unclear in *L. thandari* and probably absent in *L. samadiae*), a rectangular to tulip-shaped central tooth (slenderer in *L. vanuatuensis*), and the number of pores per granules is usually no higher than five (up to 10 in *L. boucheti*, up to eight in *L. dykei*, up to seven in *L. samadiae*, and up to nine in *L. wui*). Organic aesthete caps are only recorded so far for the following species in this group: *L. boucheti*, *L. samadiae* and *L. schwabei*.

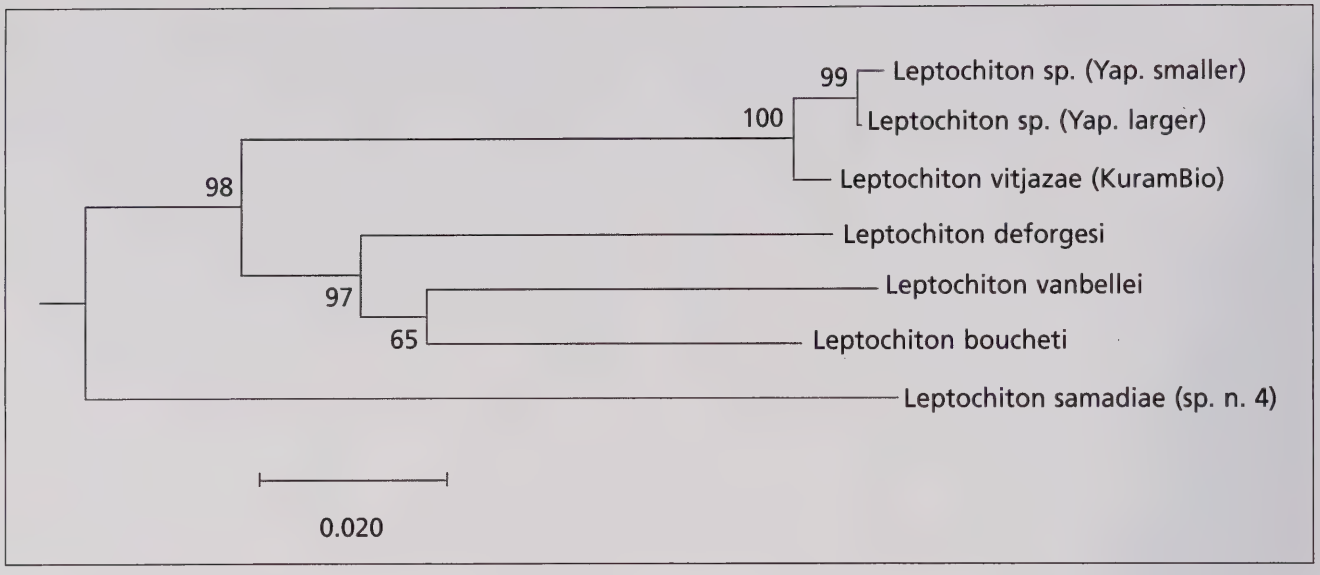

Fig. 8. Selected subtree of a Neighbour-joining phylogram for the COI. Bootstrap values above 50% are indicated.

Fig. 8. Sottoalbero selezionato di un filogramma di giunzione vicino per il COI. Sono indicati valori di Bootstrap superiori al 50%.

As stated above, it is noteworthy to mention that the few available genetic data (Sigwart et al. 2011, Wu et al. 2018) show a support for this group (inferred from COI and 28S rDNA for the following species: *Leptochiton* sp. of Wu et al. 2018, *L. boucheti*, *L. vanbellei*, *L. deforgesi*, and *L. samadiae*). Not supported however is *L. longisetosus*, which builds a sister group to a clusters comprising of *L. saitoi* Sirenko, 2001, *L. juvenis* (Leloup, 1981), and *L. vaubani* Kaas, 1991.

There are two deep water species from the Indian Ocean, which are also plant associated and superficially resemble members of the *L. vitjazae* group: *L. benthedi* (Leloup, 1981) and *L. kurnilatus* Kaas, 1985. Unfortunately, they could so far not be re-examined, but *L. kurnilatus* was described having six gills. Nothing is known about the gills and number of radula teeth rows in *L. benthedi*, but Kaas & Van Belle (1985) even considered this species as probably identical with *L. vitjazae*.

The East Pacific *Leptochiton luridus* (Dall, 1902) also shows valve morphologies similar to species of the *L. vitjazae* group and also the radula is alike (BS examination), but the number of gills is unknown.

It is interesting to note that the known distribution of *L. vitjazae* in the Pacific deep-sea trenches seems to follow the surface currents; e.g. the South Equatorial Current, the North Equatorial Current and the Kuroshio Current (**Fig. 7**). It is likely that this dependence can be explained by the spread of floating wood, which serves as the main substrate and source of food at great depths.

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References

Belyaev G.M., 1966. *Bottom fauna of the ultraabyssal depths of the world ocean*. Nauka, Moscow, 247 pp.

Belyaev G.M., 1983. Animals and plants, previously unknown to science, described from the R/V "Vityaz" collections, in Monin A.S., Rass T.S., Bezrukov P.L., Vinogradov M.E., Dobrovolsky A.D., Lisitzin A.P. & Filatova Z.A. (eds), *Research vessel Vityaz and her expeditions 1949-1979*. Nauka, Moscow: 268-323.

Belyaev G.M., 1989. *Deep-sea Ocean Trenches and their fauna*. Nauka, Moscow, 255 pp.

Belyaev G.M. & Mironov A.N., 1977. Bottom fauna of the West Pacific deep-sea trenches. *Transactions of the P. P. Shirshov Institute of Oceanology*, **108**: 7-24, pls 1-3.

Bouchet P., Héros V., Lozouet P. & Maestrati P., 2008. A quarter-century of deep-sea malacological exploration in the South and West Pacific: Where do we stand? How far to go? in Héros V., Cowie R.H. & Bouchet P. (eds), *Tropical Deep-Sea Benthos*. volume 25. *Mémoires du Muséum national d'Histoire naturelle*, **196**: 9-40.

Ferreira A.J., 1980. A new species of *Lepidopleurus* Risso, 1826 (Mollusca: Polyplacophora) in the deep waters of the Eastern Pacific. *The Veliger*, **23**: 55-61.

Ferreira A.J., 1981. A new species of *Stenosemus* Middendorff, 1847 (Mollusca: Polyplacophora) in the abyssal Northeastern Pacific. *The Veliger*, **23**: 325-328.

Gray J.E., 1847. A list of genera of Recent Mollusca, their synonyma and types. *Proceedings of the Zoological Society of London*, Part **15**: 129-206.

Jamieson A., 2015. *The Hadal Zone: Life in the Deepest Oceans.* Cambridge University Press. https://doi.org/10.1017/CBO9781139061384

Kaas P., Jones A.M. & Gowlett-Holmes K.L., 1998. Class Polyplacophora, in Beesley P.L., Ross G.J.B. & Wells A. (eds) *Mollusca: The Southern Synthesis. Fauna of Australia. Vol. 5.* Part A. CSIRO Publishing, Melbourne: 161-194, pls 7-9.

Kaas P. & Van Belle R.A., 1980. *Catalogue of living chitons (Mollusca: Polyplacophora).* Dr. W. Backhuys Publisher, Rotterdam, 144 pp.

Kaas P. & Van Belle R.A., 1985. *Monograph of living chitons. Vol. 1. Order Neoloricata: Lepidopleurina.* E. J. Brill/W. Backhuys, Leiden, 240 pp.

Kaas P. & Van Belle R.A., 1998. *Catalogue of living chitons (Mollusca, Polyplacophora). second, revised edition.* Backhyus Publishers, Leiden, 204 pp.

Lovén S.L., 1846. Index Molluscorum litora Scandinaviae occidentalia habitantium. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar*, **3**: 135-160.

Menzies R.J. & George R.Y., 1967. A re-evaluation of the concept of hadal or ultra-abyssal fauna. *Deep Sea Research and Oceanographic Abstracts*, **14**: 703-723.

Montagu G., 1803-1805. *Testacea Britannica, or natural history of British shells, marine, land, and fresh -water, including the most minute: systematically arranged and embellished with figures.* J. S. Hollis, London, xxxvii, 1-291 (Part 1, 1803), 293-606, pls 1-16 (Part 2, 1805).

Schwabe E., 2008. A summary of reports of abyssal and hadal Monoplacophora and Polyplacophora (Mollusca). *Zootaxa*, **1866**: 205-222.

Schwabe E., Bartsch I., Błażewicz-Paszkowycz M., Brenke N., Chernyshev A.V., Elsner N.O., Fischer V., Jażdżewska A., Malyutina M.V., Miljutin D., Miljtuina M., Kamenev G.M., Karanovic I., Maiorova A. & Würzberg L., 2015. Wood-associated fauna collected during the Kuram-Bio – expedition in the North West Pacific. *Deep Sea Research Part II: Topical Studies in Oceanography*, **111**: 376-388.

Sigwart J.D., Schwabe E., Saito H., Samadi S. & Giribet G., 2011. Evolution in the deep sea: a combined analysis of the earliest diverging living chitons (Mollusca: Polyplacophora: Lepidopleurida). *Invertebrate Systematics*, **24**: 560-572.

Sigwart J.D. & Sirenko B.I., 2012. Deep-sea chitons from sunken wood in the West Pacific (Mollusca: Polyplacophora: Lepidopleurida): taxonomy, distribution, and seven new species. *Zootaxa*, **3195**: 1-38.

Sirenko B.I., 1977. Vertical distribution of chitons of the genus *Lepidopleurus* (Lepidopleuridae) and its new ultraabyssal species. *Zoologicheskii Zhurnal*, **56**: 1107-1110.

Sirenko B.I., 1988. A new genus of deep sea chitons *Ferreiraella* gen. n. (Lepidopleurida, Leptochitonidae) with a description of a new ultra-abyssal species. *Zoologicheskii Zhurnal*, **67**: 1776-1786.

Sirenko B.I., 1997. *Polyplacophora: Morphological and Ecological Peculiarities, Evolution and Systematic.* Thesis, Zoological Institute of the Russian Academy of Sciences, Sankt Peterburg, 277 pp.

Sirenko B.I., 1998. One more deep-water chiton living and feeding on sunken wood: *Leptochiton vietnamensis* sp. nov. from the South China Sea (Mollusca, Polyplacophora). *Ruthenica*, **8**: 1-6.

Sirenko B.I., 2001. Deep-sea chitons (Mollusca, Polyplacophora) from sunken wood off New Caledonia and Vanuatu, in Bouchet P. & Marshall B.A. (eds), *Tropical Deep-Sea Benthos*, volume **22**. *Mémoires du Muséum national d'Histoire naturelle*, **185**: 39-71.

Sirenko B.I., 2004. The ancient origin and persistence of chitons (Mollusca, Polyplacophora) that live and feed on deep submerged land plant matter (xylophages). *Bollettino Malacologico*, **39** [2003], Supplemento **5**: 111-116.

Sirenko B.I., 2006. New outlook on the system of chitons (Mollusca: Polyplacophora). *Venus*, **65**: 27-49.

Sirenko B.I., 2015. Shallow and deep-sea chitons of the genus *Leptochiton* Gray, 1847 (Mollusca: Polyplacophora: Lepidopleurida) from Peruvian and Chilean waters. *Zootaxa*, **4033**: 151-202.

Sirenko B.I., 2016. New, rare bathyal leptochitons (Mollusca, Polyplacophora) from the South and West Pacific, in Héros V., Strong E. & Bouchet P. (eds), Tropical Deep-Sea Benthos volume 29. *Mémoires du Muséum national d'Histoire naturelle*, **208**: 25-63.

Wang C., Zhou Y & Han J., 2018. Report of a chiton in the genus *Leptochiton* (Lepidopleurida: Lepidopleurina: Leptochitonidae) from the Yap Trench in the West Pacific Ocean. *Acta Oceanologica Sinica*, **37**: 205-208.

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Emarginula lorenzoi n. sp. from the Tuscan Archipelago (Gastropoda: Fissurellidae)

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Abstract
The new species *Emarginula lorenzoi* is described based on four shells found in shell grit trawled near Capraia island (South Ligurian Sea) at a depth of about 120 m. The new species is characterized by the lamelliform ridges, with their ends pointing perpendiculary to the base plane, instead of shell profile, and the concave base profile. Differences from the other species, mainly the polymorph *E. huzardii* Payraudeau, 1826, are discussed.

Key words
Gastropoda, *Emarginula*, new species, Recent, Mediterranean.

Riassunto
[*Emarginula lorenzoi* n. sp. dall'Arcipelago Toscano (Gastropoda, Fissurellidae)]. Viene descritta la nuova specie *Emarginula lorenzoi* sulla base di quattro esemplari rinvenuti in un campione di detrito dragato presso l'isola di Capraia (mar Ligure meridionale), alla profondità di circa 120 m. La nuova specie è caratterizzata da cingoli co-marginali lamellosi, con la sommità perpendicolare al piano basale, anziché al profilo della conchiglia, e base concava. Sono discusse le differenze dalle specie simili, specialmente con la specie polimorfa *E. huzardii* Payraudeau, 1826.

Parole chiave
Gastropoda, *Emarginula*, nuova specie, recente, Mediterraneo.

Introduction

The genus *Emarginula* Lamarck, 1801 was deeply reviewed by Piani (1985), later on *E. bonfittoi* Smriglio & Mariottini, 2001 was described, based on material from deep-sea coral bank located off Latium (Central Tyrrhenian Sea). Determination of the Mediterranean species, except the group of *E. huzardii* Payraudeau, 1826, is not difficult, therefore the finding of some specimens different from all the other Mediterranean and north-east Atlantic species, induced us to describe it as new species. The new species was found in the Tuscan Archipelago, a well studied area, mainly thanks to fisherman, who provide shell grit to local shell collectors, therefore other specimens are possibly present in the malacological collections.

Material and methods

The studied material was found in a sample of some kilograms of sediment consisting of muddy sand taken by a fishing boat using trawling net on 1997, at a depth of about 120 m off Capraia island (South Ligurian sea). The dried sediment was then sieved and the various fractions sorted out for shells under a stereo microscope. Photographs were taken with digital camera Canon EOS 1000D.

Abbreviations and acronyms: Museum of Zoology of Bologna University (MZB); Francesco Giusti private collection, Livorno (FGL); Pasquale Micali private collection, Fano (PMF); Luigi Innocenti, Pisa (LIP). For shell dimensions: H= height, measured from the shell base, not from base plane; L= length; W= width.

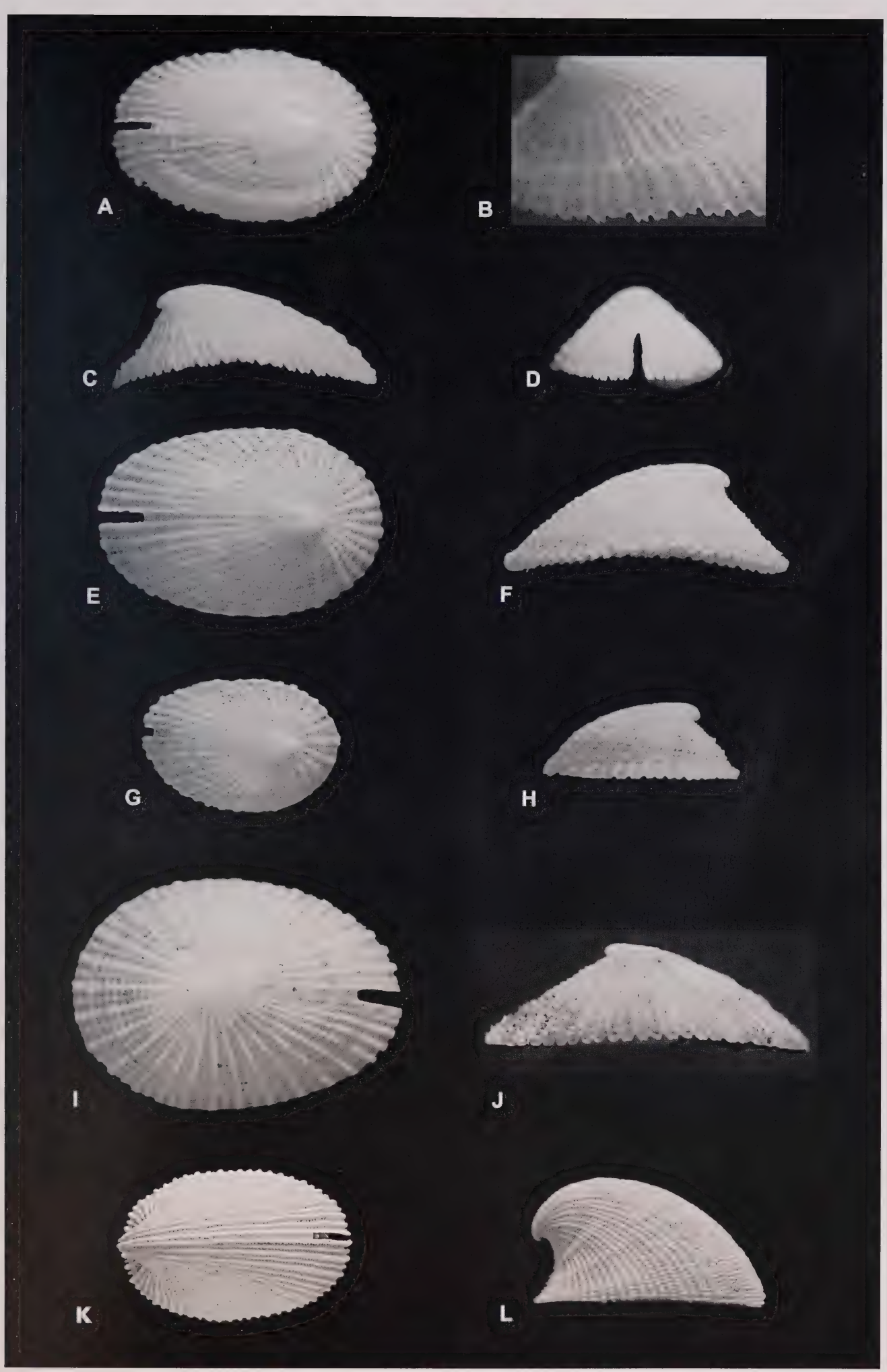
Systematics

Superfamily Fissurelloidea Fleming, 1822
Family Fissurellidae Fleming, 1822
Genus *Emarginula* Lamarck, 1801
(type species *Emarginula conica* Lamarck, 1801)

Emarginula lorenzoi n. sp.
(Fig. 1. A-E)

Fig. 1. A-D. *Emarginula lorenzoi* n. sp., holotype, off Capraia island, 120m, type locality, length = 17 mm (MZB60253). **E-F**. *Emarginula lorenzoi* n. sp., Paratype 1, type locality, length = 18 mm (FGL). **G-H**. *Emarginula lorenzoi* n. sp., Paratype 2, type locality, length = 10.5 mm (PMF). **I-J**. *Emarginula huzardii* Payraudeau, 1826, Linosa island, 70 m, length = 22 mm (PMF). **K-L**. *Emarginula adriatica* O.G. Costa, 1829, Tuscan Archipelago, 200 m, length = 15 mm (PMF).

Fig. 1. A-D. *Emarginula lorenzoi* n. sp., olotipo, al largo dell'isola Capraia, 120m, località tipo, lunghezza = 17 mm (MZB60253). **E-F**. *Emarginula lorenzoi* n. sp., Paratipo 1, località tipo, lunghezza = 18 mm (FGL). **G-H**. *Emarginula lorenzoi* n. sp., Paratipo 2, località tipo, lunghezza = 10.5 mm (PMF). **I-J**. *Emarginula huzardii* Payraudeau, 1826, isola Linosa, 70 m, lunghezza = 22 mm (PMF). **K-L**. *Emarginula adriatica* O.G. Costa, 1829, Arcipelago Toscano, 200 m, lunghezza = 15 mm (PMF).



Emarginula lorenzoi n. sp. from the Tuscan Archipelago (Gastropoda: Fissurellidae)

Type material

Holotype, LxWxH = 17 x 11 x 6 mm, type locality (Museo di Zoologia dell'Università di Bologna, n° MZB60253). **Fig. 1 A-D**.
Paratype 1, LxWxH = 18 x 12 x 6.2, mm, type locality (FGL), **Fig. 1 E-F**.
Paratype 2, LxWxH = 10.5 x 7 x 4, mm, type locality (PMF), **Fig. 1 G-H**.
Paratype 3, LxWxH = 17.3 x 11.2 x 6, mm, type locality (LIP).
All the examined specimens are empty shells.

Type locality

Off Capraia island (South Ligurian Sea), about 120 m water depth.

Etymology

Dedicated to Lorenzo, grandson of the first Author.

Description of holotype

Shell white, moderately solid, sub-elliptical, cap-shaped, with the beak curving backwards and ending in apical whorls. There is about one protoconch whorl, having a diameter of about 200 µm, with a well marked protoconch-teleoconch boundary. The tip of the spire faces to the right and its axis is roughly parallel to the plane of aperture. The beak lies, in side view, at about 85% of total shell height, while in apical view lies at about 82% of the total shell length, behind the anterior margin. From the centre of anterior margin, a narrow slit extends about 25% of the way to the beak and is continued to that point as a slit band filled with about 45 curved lamellae, irregularly spaced. Both slit and slit band have parallel sides, the margin of the latter is a little more raised than the ribs. The anterior shell profile is gently convex, the lateral quite straight and the posterior slightly concave. The sculpture consists of radial ribs and co-marginal lamelliform ridges. The anterior and posterior ribs run straight to the shell margin, while the lateral ones curving backwards. Some secondary, weaker ribs, are sometimes present in the interspaces. In the holotype there are about 37 primary ridges, and about 17 secondary, irregularly distributed. At the margin about half of the secondary ribs are as strong as the primary ones. The ridges are lamelliform, about 40 in number, producing a squarish reticulate pattern. When passing over the ribs, the ridges maintain the lamelliform shape, with their tip pointing perpendicular to base plane. The ridges are very close near the beaks, than distance is increasing, but they are irregularly spaced and sometimes are quite attached each other, some stronger, some other weaker. Aperture oval, the lip sinuous by the ends of ribs. In side view the base plane is curved, with a maximum distance from base plane of about 15% of the real height. Size: L= 17 mm, W = 11 mm, H = 6 mm.

Variability

Variability is described based on the comparison with paratypes. The beak lies from 79% to 82% of the total shell length, behind the anterior margin. The W/L ratio is slightly variable, between 0.66 and 0.67. The base profile is quite flat in the Paratype 2 (**Fig. 1 H**), that is smaller than other specimens.

Distribution

The species is known from the type locality only.

Discussion

The new species is characterised by the lamellose ridges pointing perpendicularly to basal plane (**Fig. 1. B**), a character present, among the Mediterranean and North-east Atlantic species, only in *E. huzardii* Payraudeau, 1826. The new species differs from *E. octaviana* Coen, 1939 for the lamellose ridges, the much finer sculpture, the larger size and the distribution in deep waters instead of littoral. *Emarginula adriatica* O. G. Costa, 1829 (**Fig. 1. K-L**) is frequent in deep waters (200-400 m) of Tuscan Archipelago and reaches slightly smaller dimensions (Piani, 1985); the new species differs for the lamellose ridges, the more central position of the apex, the more depressed shell (H/L about 0.4 against about 0.6 in specimens over 10 mm long), the lower number of ribs (about 54 against about 80), the less dense sculpture and the concave instead of flat base.

Emarginula lorenzoi shows some resemblance with the specimen reported by Manousis & Galinou-Mitsoudi (2014) as *E. decorata* Deshayes, 1863, an alien Indopacific species. The report is based on a single living individual found at Chalkidiki Peninsula (Greece), at a depth of 120, over a sponge. According to WORMS (accessed on 30 June 2019) *E. decorata* is distributed along Eastern Africa, Arabian Gulf and Red Sea. Photo of *E. decorata* holotype (MNHN number 2000-4754), length 8.5 mm (while original description indicates a length of 6 mm), is available in http://coldb.mnhn.fr/catalognumber/mnhn/im/2000-4754. The shell found in Greece is very large (length 16.55 mm), about twice the other literature data and the comparison also with the figured and photographed holotype becomes difficult. By comparing data and figures from Dehayes (1863), the photo of the holotype, the photo by Herbert (2015) and the photo published in http://vieoceane.free.fr/mollusques/intro_frame.htm, illustrating a specimen coming from Reunion, as the type, with the figured specimen from Greece, some differences are visible, in particular the outline of the shell which in the specimen of Manouis & Galinou-Mitsoudi (2014) tends to enlarge posteriorly while in the original figure, the type and other images, the sides are sub-parallel, the number of the principal costae varying from 29 to 31 in all the specimens examined and numbering 40 (57 if we consider also the sec-

ondary ones) in the Greek shell, as well as the base, that in *E. decorata* is flat instead of concave. Nothing can be said on the position of the apex which is very variable ranging from 1/7 to about 1/4 (1/7 in the photographed holotype versus 1/3.7 in the original drawing). A last consideration about the fact that the specimen found in Greece was living at a depth of 120 m, so it is not a littoral species. These are the reasons why we doubt the correct identification of Manouis & Galinou-Mitsoudi (2014) and believe that their specimen could belong to the new species.

The comparison with *E. huzardii* shall consider that the shell outline varies during growth, changing from an outline with almost parallel sides and apex positioned towards the posterior side, to a remarkably curved sides and sub-central apex. Piani (1985) state: "La variabilità morfologica è grande, soprattutto tra stadi giovanili ed adulti, nei quali la posizione dell'apice diviene sempre più centrale [The morphological variability is remarkable, mainly between small and large specimens, where the apex tends to be more and more central]". The species *E. crebrisculpta* Coen, 1939 from Gulf of Naples and *E. divae* Aartsen & Carrozza, 1996 from Israel are considered by Portalatina (2009) possible morpha of *E. huzardii*, while other Authors (e.g. Cecalupo & Quadri, 1996) consider *E. crebrisculpta* a valid species. The several specimens figured by Piani (1985), Portalatina (2009) and Cossignani & Ardovini (2011), well show the variability of this species. The new species shares with *E. huzardii* (**Fig. 1. I-J**) the lamellose co-marginal ridges, but clearly differs for having these much more prominent, the apex positioned toward the posterior margin, while in the former of similar dimension it is sub-central, the general outline less orbicular, the ribs and ridges finer and closer, the ridges almost double in number, creating a lattice with smaller squares. In addition the new species has few and scattered secondary ribs, while *E. huzardii* has a much more regular alternating of strong and weak ribs.
Emarginula guernei Dautzenberg & Fischer, 1896 is the only species distributed in North-east Atlantic to show some resemblance with the new species. It is reported for the Azores, at a depth of 454 m. The new species differs for the different position of the apex, that, in apical view, does not reach the posterior margin, and the lamellose instead of cord-like ridges without tubercles at the crossings.

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References

Cecalupo A. & Quadri P., 1996. Contributo alla conoscenza malacologia per il nord dell'isola di Cipro (Terza e ultima parte). *Bollettino Malacologico*, **31**[1995] (5-8): 95-118

Cossignani T. & Ardovini R., 2011. *Malacologia Mediterranea*. L'Informatore Piceno, Ancona; 536 pp., 7500 figg.

Deshayes G.P., 1863. Catalogue des mollusques de l'Ile de la Réunion (Bourbon). In Maillard, L. (Ed.) *Notes sur l'Ile de la Réunion (Bourbon)*. Mollusques. Dentu, Paris, pp. 1-144.

Herbert D.G., 2015. An annotated catalogue and bibliography of the taxonomy, synonymy and distribution of the Recent Vetigastropoda of South Africa (Mollusca). *Zootaxa*. **4049** (1): 1-98.

Manousis T. & Galinou-Mitsoudi S., 2014. New gastropod records for the Eastern Mediterranean Sea and one new alien (*Emarginula decorata* Deshayes, 1863) for the Mediterranean Sea from NW Aegean Sea, Greece. *Journal of Biological Research -Thessaloniki*, **21**: 20.

Piani P., 1985. Revisione del genere *Emarginula* Lamarck, 1801in Mediterraneo. *Lavori della Società Italiana di Malacologia*, [1984] **21**: 193-238.

Portalatina M., 2009. Analisi concometrica sul complesso di specie *Emarginula crebrisculpta* Coen, 1939 - *Emarginula divae* Aartsen & Carrozza, 1996 - *Emarginula huzardii* Payraudeau, 1826 (Gastropoda: Fissurellidae). *Thalassia Salentina*, **31** [2008]: 79-91.

World Register of Marine Species (WoRMS). http://www.marinespecies.org, accessed 30 Jun 2019.

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First record of *Acanthochitona pilosa* Schmidt-Petersen, Schwabe & Haszprunar, 2015 (Mollusca: Polyplacophora) in Spain and Algeria

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Abstract

Acanthochitona pilosa Schmidt-Petersen, Schwabe & Haszprunar, 2015, originally described from southern France, is here reported for the first time from Spain and Algeria. The specimens from Oran were attached on the shell of living *Cymbula safiana* (Lamarck, 1819), together with *Lepidochitona monterosatoi* Kaas & Van Belle, 1981. *A. oblonga* Leloup, 1981 is recorded for the first time from the Latium Region (Italy, Central Tyrrhenian Sea). Single plates of *A. crinita* (Pennant, 1777) are reported for the first time in Sardinia.

Key words

First record, Mediterranean Sea, chitons.

Riassunto

Acanthochitona pilosa Schmidt-Petersen, Schwabe & Haszprunar, 2015, descritto dalla Francia meridionale, è qui riportato per la prima volta da Spagna e Algeria. Gli esemplari da Orano sono stati rinvenuti assieme a *Lepidochitona monterosatoi* Kaas & Van Belle, 1981 attaccati alle conchiglie di *Cymbula safiana* (Lamarck, 1819) viventi. *A. oblonga* Leloup, 1981 è riportata per la prima volta dal Lazio (Italia). Piastre isolate di *A. crinita* (Pennant, 1777) sono infine riportate per la prima volta in Sardegna.

Parole chiave

Primo ritrovamento, Mar Mediterraneo, chitoni.

Introduction

Acanthochitona pilosa Schmidt-Petersen, Schwabe & Haszprunar, 2015 was recently described (Schmidt-Petersen et al., 2015) from southern France. It is easily diagnosed by its peculiar morphology, and lives in exposed and well oxygenated waters (not preferentially in sciaphilic conditions like the other Mediterranean congeners). We report here the first records of this species outside its type locality, based on live specimens collected by one of us in Algeria, and in Spain based on disarticulated plates. We have also made an extensive, yet possibly non-exhaustive bibliographic search of the Italian records of two other species of the same genus, *A. crinita* (Pennant, 1777) and *A. oblonga* Leloup, 1981. Based on this search, we also report here the first records for Sardinia of *A. crinita*, and the first records for Latium of *A. oblonga* Leloup, 1981. Current systematics is based on the World Register of Marine Species (MolluscaBase). Photographs have been taken with a Sony Cyber-Shot digital camera mounted on a Kyowa KBS stereomicroscope, edited with the Combine-Z software (Hadley, 2006).

Systematics

Class Polyplacophora Gray, 1821
Subclass Neoloricata Bergenhayn, 1955
Superfamily Cryptoplacoidea
H. Adams & A. Adams, 1858

Family Acanthochitonidae Pilsbry, 1893
Genus *Acanthochitona* Gray, 1821: 234

Type-species: *Chiton fascicularis* Linné, 1767 (by monotypy)

Acanthochitona pilosa Schmidt-Petersen, Schwabe & Haszprunar, 2015
(Fig. 1. A-D, Fig. 3)

Acanthochitona pilosa Schmidt-Petersen et al., 2015: 12

Type locality

France, Banyuls sur Mer (42°28′57″ N – 03°08′13″ E).

Material examined

Algeria, port of Oran, on *Cymbula safiana* (Lamarck, 1819), 1 m depth (B. Amati leg.), 35°42′46.77″ N – 0°38′45.70″ W, 9 specimens (**Fig. 1. A-D**) (B. Amati collection, Rome). Spain, Cadaqués, Girona, 32.5 m depth, bioclastic sand, 2 plates (B. Amati collection, Rome).

Remarks

The material from Oran was already reported by Amati (1979: 46) as *Acanthochitona fascicularis* (Linné, 1767). The specimens were attached to the dorsal surface of

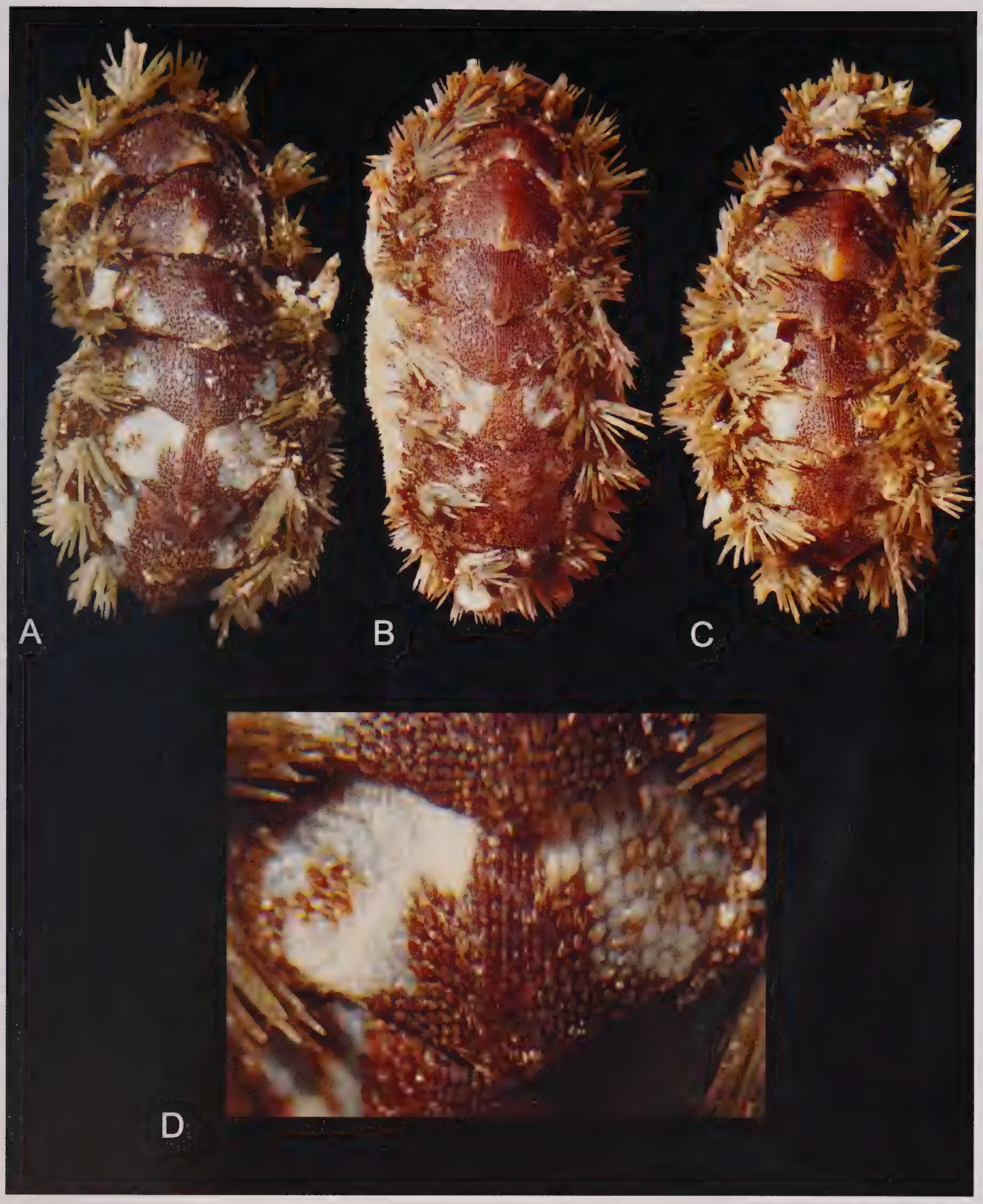

Fig. 1. A-D. A-C. *Acanthochitona pilosa* Schmidt-Petersen, Schwabe & Haszprunar, 2015. Algeria, Oran, 35°42'46.77" N, 0°38'45.70" W, length 7 mm (**A**), 6.5 mm (**B** and **C**). **D**. close-up of plate VI (same specimen as **A**) (B. Amati collection).

Fig. 1. A-D. A-C: *Acanthochitona pilosa* Schmidt-Petersen, Schwabe & Haszprunar, 2015. Algeria, Oran, 35°42'46.77" N, 0°38'45.70" W, lunghezza 7 mm (**A**), 6.5 mm (**B** and **C**). **D.** particolare della piastra VI (stesso esemplare di **A**) (collezione B. Amati).

the shell of *Cymbula safiana* (Lamarck, 1819), collected on large boulders on the dock of the port of Oran. The rocks and the limpets were covered by concretions, the most abundant being the coral alga *Ellisolandia* cf. *elongata* (J. Ellis & Solander) K.R. Hind & G.W. Saunders, 2013. Size of the specimens ranged from 4.5 to 10 mm in length. The Algerian specimens show rather constant features, both in form and in coloration, conforming to those of the type series, except for the white specks on the plates, which in our specimens have a bluish-white hue (**Fig. 1. D**). Almost all specimens have bilateral bluish-white blotches on the posterior plates, never on the

first 3 plates; a monochrome white specimen was also found.

Acanthochitona crinita (Pennant, 1777)
(Fig. 2. A, Fig. 3)

Chiton crinitus Pennant, 1777: 71; pl. 36 fig. 1, A1

Material examined

Italy, Santa Marinella (Rome) 42°02′15.45″ N – 11°55′04.48″ E, under stone 0.50 m depth, 22.vi.2007 (B. Amati leg. et coll.) 3 specimens (**Fig. 2. A**); Nettuno (Rome) 41°27′18″ N – 12°39′38″ E, beached, vii.1984 (B. Amati leg. et coll.) 7 plates. Sardinia, Cala Gonone (NU), 40°16′57″ N – 09°38′17″ E, trawling net residuals, viii.2010 (B. Amati legit et coll.) 4 plates; Bosa Marina, bioclastic sand beach (M. Amati legit) 2 plates (B. Amati coll.); Sicily, Punta Asparano (SR), 36°59′09″ N – 15°16′04″ E, beached bioclastic sediment, ix.1985 (M. Lombardo legit) 1 plate (B. Amati coll.); Ognina (SR), 36°58′49″ N – 15°15′38″ E, beached bioclastic sediment, 10.x.1982 (M. Lombardo legit) 6 plates (B. Amati coll.); Cannizzaro (CT), 30-40 m depth, bioclastic sediment 2 plates (B. Amati coll.); Salina Is., 35 m depth 'gamberetti' cave, bioclastic sediments vii.2002 (M. Oliverio legit) 5 plates (B. Amati coll.); Lampedusa Is, 30 m depth bioclastic sediment, 30.iv.1991 (M. Oliverio legit) 5 plates (B. Amati coll.).

Remarks

The largest specimen from Santa Marinella is 14 mm long. Previously recorded in Italy from the following regions: Veneto, Liguria, Tuscany, Latium, Calabria, Apulia and Sicily (see **Fig. 3**). This is the first record for Sardinia (based on disarticulated plates).

Acanthochitona oblonga Leloup, 1981
(Fig. 2. B, Fig. 3)

Acanthochiton oblongus Leloup, 1981: 1-3; pl. 1 fig. 1

Material examined

Italy, Nettuno (Rome), 41°27′15.32″ N – 12°38′54.78″ E, under stone 0.50 m depth, 24.vii.1977 (B. Amati leg. et coll.) 1 specimen (**Fig. 2. B**); 41°27′18″ N – 12°39′38″ E, beached, vii.1984 (B. Amati leg. et coll.) 2 plates.

Remarks

Length 11.5 mm. This is the first record for the Latium Region. Previously recorded in Italy from Tuscany, Apulia, Sicily, Lampedusa Is. (see **Fig. 3**).

Discussion

Recently, several authors have revised the systematics of the 4 Mediterranean species of *Acanthochitona* (Mollusca Base, 2019): *A. fascicularis* (Linné, 1767), *A. crinita* (Pennant, 1777), *A. oblonga* Leloup, 1981 and *A. pilosa* Schmidt-Petersen, Schwabe & Haszprunar, 2015 (e.g. Kaas, 1985; Dell'Angelo & Smriglio, 1999; Bonfitto et al. 2011; Schmidt-Petersen et al., 2015).
A. fascicularis and *A. crinita* had a troubled taxonomic life (Kaas, 1985), despite their specific separation never raised any problems. *Acanthochitona oblonga*, sometimes considered as a synonym of *A. crinita* (Kaas, 1985; Del-

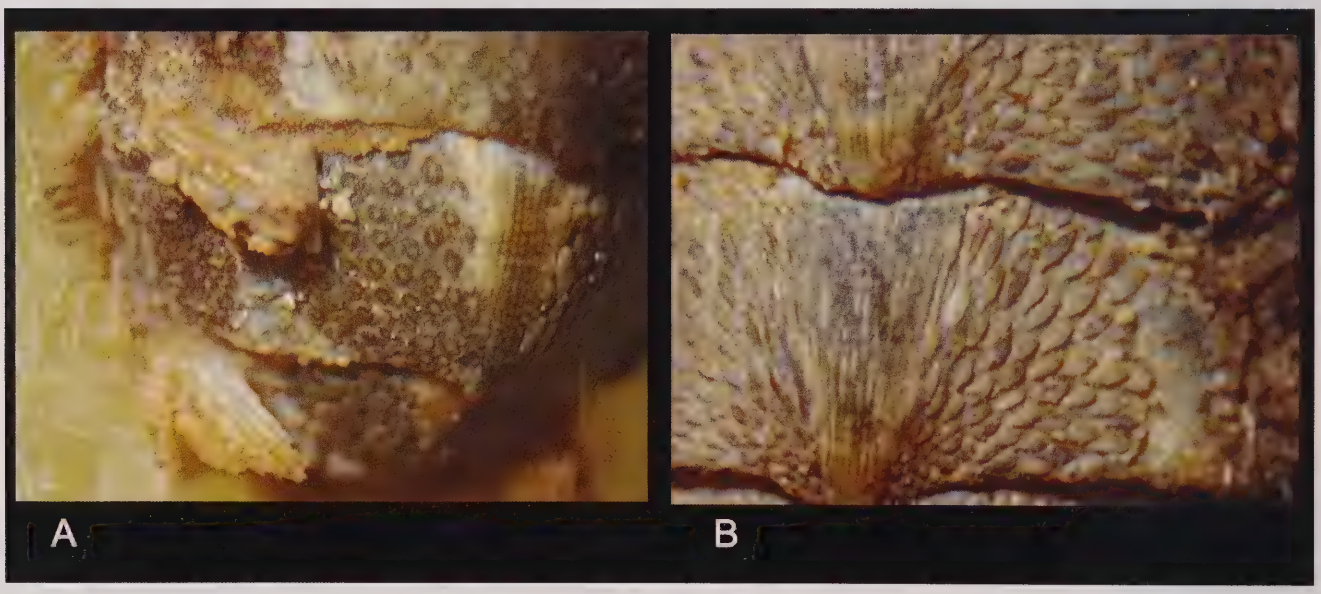

Fig. 2. A. *Acanthochitona crinita* (Pennant, 1777), Italy, Santa Marinella, 42°02′15.45″N – 11°55′04.48″E, – 0.50 m, length 14 mm, close-up of plate VII (B. Amati collection). **B**. *Acanthochitona oblonga* Leloup, 1981. Italy, Nettuno, 41°27′15.32″N – 12°38′54.78″E, – 0.50 m, length 11.5 mm, close-up of plate IV (B. Amati collection).

Fig. 2. A. *Acanthochitona crinita* (Pennant, 1777), Italia, Santa Marinella, 42°02′15.45″N – 11°55′04.48″E, – 0.50 m, lunghezza 14 mm, particolare della piastra VII (collezione B. Amati). **B**. *Acanthochitona oblonga* Leloup, 1981. Italia, Nettuno, 41°27′15.32″N – 12°38′54.78″E, – 0.50 m, lunghezza 11.5 mm, particolare della piastra IV (collezione B. Amati).

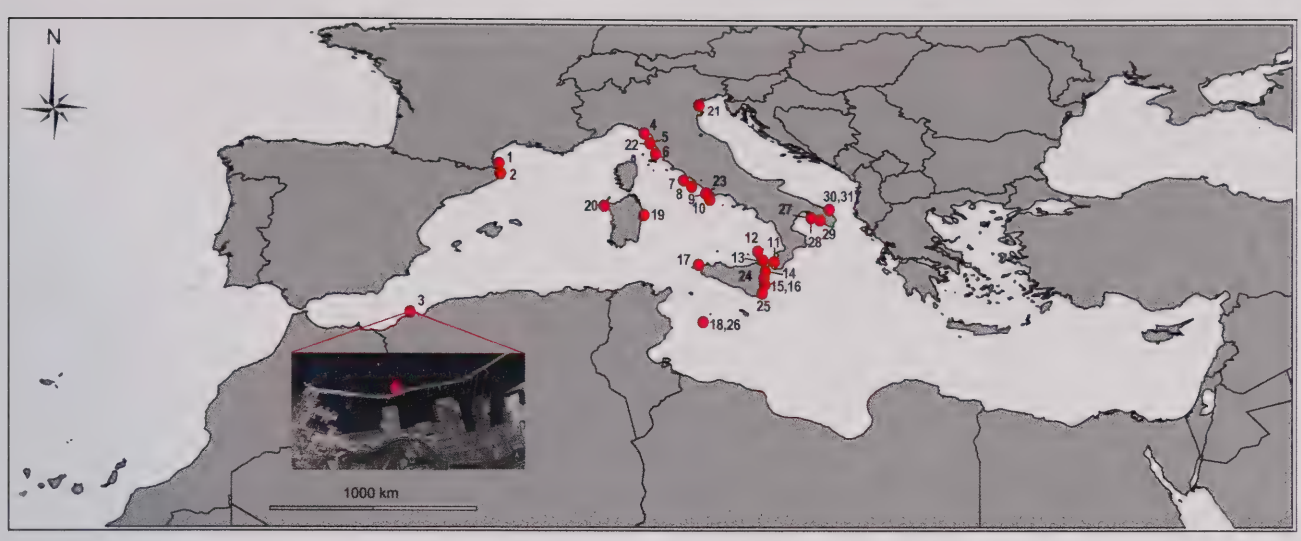

Fig. 3. Known records of *A. pilosa*: 1) Banyuls sur Mer (Schmidt-Petersen et al., 2015); 2) Cadaqués (this work) (B. Amati collection); 3) port of Oran (this work) (B. Amati collection). Italian known records of *A. crinita*: 4) La Spezia (Dell'Angelo & Smriglio, 1999); 5) Livorno (Bogi et al., 1981; Dell'Angelo, 1985); 6) Gulf of Baratti (Scaperotta et al., 2015); 7) Santa Marinella (this work) (B. Amati collection); 8) Secche di Tor Paterno (Albano, 2011); 9) Nettuno (this work) (B. Amati collection); 10) Zannone Is. (Fumanti, 2014); 11) Scilla (Vazzana, 2010; Giacobbe & Renda, 2018); 12) Salina Is. (this work) (B. Amati collection); 13) Villafranca Tirrena (Bonfitto et al., 2011); 14) Cannizzaro (this work); 15) Punta Asparano (this work) (B. Amati collection); 16) Ognina (this work) (B. Amati collection); 17) Lido S. Giuliano, Trapani (Dell'Angelo & Smriglio, 1999); 18) Lampedusa Is, (this work) (B. Amati collection); 19) Cala Gonone (this work) (B. Amati collection); 20) Bosa Marina (this work) (B. Amati collection); 21) Laguna di Venezia (Cesari, 1994). Italian known records of *A. oblonga*: 22) Livorno, (Savona & Carnieri, 1985); 23) Nettuno (this work) (B. Amati collection); 24) Siracusa (Dell'Angelo & Cuppini, 1983); 25) Vendicari (Dell'Angelo & Cuppini, 1983; Gaglini in Settepassi, 1985); 26) Lampedusa Is. (Dell'Angelo & Cuppini, 1983); 27) Marina di Lizzano (Bonfitto et al., 2011); 28) Campomarino (Dell'Angelo & Cuppini, 1983; Bonfitto et al., 2011); 29) Porto Cesareo (Dell'Angelo & Cuppini, 1983); 30) Roca Li Posti (Bonfitto et al., 2011); 31) San Foca (Bonfitto et al., 2011; Baschieri et al., 1992; Baschieri, 1994)

Fig. 3. Reperti noti di *A. pilosa*: 1) Banyuls sur Mer (Schmidt-Petersen et al., 2015); 2) Cadaqués (this work) (collezione B. Amati); 3) porto di Oran (questo lavoro) (collezione B. Amati). Reperti italiani di *A. crinita*: 4) La Spezia (Dell'Angelo & Smriglio, 1999); 5) Livorno (Bogi et al., 1981; Dell'Angelo, 1985); 6) Golfo di Baratti (Scaperotta et al., 2015); 7) Santa Marinella (questo lavoro) (collezione B. Amati); 8) Secche di Tor Paterno (Albano, 2011); 9) Nettuno (questo lavoro) (collezione B. Amati); 10) Zannone (Fumanti, 2014); 11) Scilla (Vazzana, 2010; Giacobbe & Renda, 2018); 12) Salina (questo lavoro) (B. Amati collection); 13) Villafranca Tirrena (Bonfitto et al., 2011); 14) Cannizzaro (questo lavoro); 15) Punta Asparano (questo lavoro) (collezione B. Amati); 16) Ognina (questo lavoro) (collezione B. Amati); 17) Lido S. Giuliano, Trapani (Dell'Angelo & Smriglio, 1999); 18) Lampedusa (questo lavoro) (collezione B. Amati); 19) Cala Gonone (questo lavoro) (collezione B. Amati); 20) Bosa Marina (questo lavoro) (collezione B. Amati); 21) Laguna di Venezia (Cesari, 1994). Record italiani noti di *A. oblonga*: 22) Livorno, (Savona & Carnieri, 1985); 23) Nettuno (questo lavoro) (collezione B. Amati); 24) Siracusa (Dell'Angelo & Cuppini, 1983); 25) Vendicari (Dell'Angelo & Cuppini, 1983; Gaglini in Settepassi, 1985); 26) Lampedusa (Dell'Angelo & Cuppini, 1983); 27) Marina di Lizzano (Bonfitto et al., 2011); 28) Campomarino (Dell'Angelo & Cuppini, 1983; Bonfitto et al., 2011); 29) Porto Cesareo (Dell'Angelo & Cuppini, 1983); 30) Roca Li Posti (Bonfitto et al., 2011); 31) San Foca (Bonfitto et al., 2011; Baschieri et al., 1992; Baschieri, 1994).

l'Angelo & Smriglio, 1999), has recently been retained and confirmed as a valid species based on morphological and molecular evidence (Bonfitto et al., 2011).

Three of the four Mediterranean species of *Acanthochitona* occur in the Algerian waters: *A. fascicularis* (Kass, 1985; Bonfitto et al., 2011), *A. crinita* (Bonfitto et al., 2011) and *A. pilosa* (in this work).

A. crinita and *A. oblonga*, have already been recorded in the Italian fauna, albeit rarely (e.g. Bogi et al., 1981; Dell'Angelo & Cuppini, 1983; Gaglini in Settepassi, 1985; Dell'Angelo, 1985; Savona & Carnieri, 1985; Baschieri et al., 1992; Cesari, 1994; Baschieri, 1994; Dell'Angelo & Smriglio, 1999; Vazzana A., 2010, Albano, 2011, Bonfitto et al., 2011, Fumanti, 2014; Scaperrotta et al., 2015; Giacobbe & Renda, 2018). In the regional malacological checklist of the Latium Region (Nofroni, 1986) only the common *A. fascicularis* was reported. We add here the first record of *A. oblonga* from Latium, and of *A. crinita* from Sardinia.

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References

Albano P., 2011. *Molluscs of the marine protected area "Secche di Tor Paterno"*. Tesi, Università di Bologna, Dottorato di Ricerca in biodiversità ed evoluzione: 307 pp (unpublished).

Amati B., 1979. Osservazioni sulla malacofauna vivente sul substrato rigido del molo di Orano. *Notiziario del C.I.S.Ma.*, **1** (1): 45-50.

Baschieri L., 1994. Un'insolita concentrazione di due specie di Poliplacofori. *La Conchiglia*, Roma, **26** (270): 40-42.

Baschieri L., B. Dell'Angelo & S. Palazzi, 1992. Recenti ritrovamenti di Polyplacophora anomali nel Mediterraneo. *Bollettino Malacologico*, **28**: 65-68.

Bogi C., Coppini M. & Margelli M., 1981. Molluscan fauna of the central Tyrrhenian Sea. Poliplacophora: Parte 2. *La Conchiglia*, **13** (142, 143): 3-7.

Bonfitto A., Dell'Angelo B., Evangelisti F. & Sabelli B.,

2011. The genus *Acanthochitona* (Mollusca: Polyplacophora) in the Mediterranean Sea: morphological and molecular data. *Scientia Marina,* **75** (1): 171-180.

Cesari P., 1994. *I Molluschi della Laguna di Venezia. Serie "Collana Ambiente" n. 5*, Arsenale Editrice, Venezia: 190 pp, 60 tav

Dell'Angelo B., 1985. Ipermeria in *Acanthochitona* (Mollusca: Polyplacophora) delle coste livornesi. *Quaderni del Museo di Storia Naturale di Livorno* **5** (1984): 77-80.

Dell'Angelo B. & Cuppini S., 1983. Prima segnalazione di *Acanthochitona oblonga* Leloup, 1981 lungo le coste italiane. *Bollettino Malacologico,* **19**: 77-7.

Dell'Angelo B. & Smriglio C., 1999. *Chitoni viventi del Mediterraneo. Evolver*, Roma. (English edition, 2001. *Living chitons from the Mediterranean Sea*). 255 pp., Roma *Arti Grafiche La Moderna.*

Fumanti B., 2014. Contribution to the knowledge of the benthic molluscan thanatocoenosis of Zannone Island (Pontine Archipelago, Latium Italy). *Biodiversity Journal*, **5** (2): 97-106.

Gaglini A., 1985. Classe Amphineura. In: F. Settepassi (ed.), (1972), *Atlante Malacologico. I Molluschi Marini viventi nel Mediterraneo.* Vol. III, 19 pp. INIVAG, Roma.

Giacobbe S. & Renda W., 2018. Infralittoral molluscs from the Scilla cliff (Strait of Messina, Central Mediterranean). *Biodiversity Journal*, **9** (3): 255-270.

Gray J. E., 1821. A natural arrangement of Mollusca, according to their internal structure. London *Medical Repository.* **15**: 229-239.

Hadley A., 2006. Combine ZP public domain image processing software. Available from https://web.archive.org/web/20160221032141/http://www.hadleyweb.pwp.blueyonder.co.uk/

Kaas P., 1985. The genus *Acanthochitona* Gray, 1821 (Mollusca, Polyplacophora) in the north-eastern Atlantic Ocean and in the Mediterranean Sea, with designation of neotypes of *A. fascicularis* (L., 1767) and of *A. crinita* (Pennant, 1777). *Bulletin du Muséum National d'Histoire Naturelle.* Paris, 4e série, 7, section A, n° 3: 579-609.

Leloup E., 1981. *Acanthochiton oblongus* sp. nov. *Mémoires de l'Institut Royal des Sciences Naturelles de Belgique,* **53** (5): 1-3

MolluscaBase, 2019. MolluscaBase. *Acanthochitona* Gray, 1821. Accessed through: World Register of Marine Species at:
http://www.marinespecies.org/aphia.php?p=taxdetails&id=137613 on 2019-04-10.

Nofroni I., 1986. Elenco Molluschi Conchiferi del Lazio in Annuario 86, Supplemento al n. 212-213. *La Conchiglia*: 16 pp + 82 pp.

Pennant T., 1777. *British Zoology, vol. IV. Crustacea. Mollusca. Testacea. London.* i-viii, 1-154, Plates 1-93.

Savona S. & Carnieri E., 1985. Prima segnalazione di *Acanthochitona oblonga* Leloup, 1981 nelle acque toscane (Amphineura: Acanthochitonidae). *Notiziario del C.I.S.Ma.,* **5** (1-2): 36-38 [1983].

Scaperrotta M., Bartolini S. & Bogi C., 2015. Accrescimenti. *Stadi di accrescimento dei molluschi marini del Mediterraneo.* Volume VII, 192 pp.

Schmidt-Petersen J., Schwabe E. & Haszprunar G., 2015. *Acanthochitona pilosa* spec. nov. A new species of *Acanthochitona* Gray, 1821 from the Mediterranean (Mollusca, Polyplacophora). *Spixiana,* **38**: 11-20.

Vazzana A., 2010. La malacofauna del Circalitorale di Sicilia (Stretto di Messina). *Bollettino Malacologico*, **46** (2): 65-74.

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Euthecosomata (Mollusca: Gastropoda: Thecosomata). A taxonomic review

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Abstract

Euthecosomata Meisenheimer, 1905 are holoplanktonic Mollusca. Those with coiled or straight shell were originally classified as Limacinidae Gray, 1847 (*Limacina* Gray, 1847, *Thielea* Strebel, 1908) and Cavolinidae Gray, 1850 - Cavoliniidae Fischer, 1883 (*Creseis* Rang, 1828, *Styliola* Gray, 1850, *Hyalocylis* Fol, 1875, *Cuvierina* Boas, 1885, *Clio* Linnaeus, 1767, *Diacria* Gray, 1847, *Cavolinia* Abdlgard, 1791, *Diacavolinia* Spoel, 1987). In subsequent cladistical analyses, since a change was first observed in the latter family, the genera with conica shell, *Creseis*, *Styliola*, and *Hyalocylis* were all classified as Creseidae Rampal, 1973. In order to check this last result and to up date the taxonomy of all the Euthecosomata, it was necessary to pursue this study further in collaboration with molecular biologists. Based on COI data the Limacinidae are polyphyletic, the Cavoliniidae are poly from Bayesan or paraphyletic from ML analysis, the Creseidae are polyphyletic in both methods. Based on 28S data several traditional families are not monophyletic. In cladogenesis the Limanicidae and the Creseidae are paraphyletic, the Cavoliniidae are monophyletic. Based on COI data the straight shelled species could likely have appeared twice independently. However the 28S did not support this scenario but displayed high congruence with morphological and paleontological data for resolving the deep nodes (Corse et al. 2013).

In view of these new insights, it was proposed a new detailed taxonomy of this clade (Rampal, 2017). The Limacinidae are subdivided into three families: Limacinidae Gray, 1847, Heliconoididae n. fam. and Thieleidae n. fam. The Creseidae Rampal, 1973 are validated with two genera: *Creseis* Rang, 1828 and *Boasia* – previously – a subgenus of *Creseis* (Dall, 1889). *Styliola* and *Hyalocylis* are *incertae sedis*. The Cavoliniidae Gray, 1850 are subdivided into four subfamilies: Cuvierininae Spoel, 1967, Cliinae Jeffreys, 1869, Diacriinae Rampal, 2017 and Cavoliniinae Gray, 1850. The Creseidae Rampal, 1973 and the Cavoliniidae Gray, 1850 belong to the Cavolinioidea Gray, 1850. The rank of most species is confirmed. The following genera are proposed or re-established: *Telodiacria* n. gen. (Rampal, 2017), *Hyalaea* de Blainville, 1821, *Boasia* Dall, 1889. The fossil *Vaginella* Daudin, 1800 is placed in the Cuvierininae. The fossil *Altaspiratella* Korobkov, 1966 is no longer reguarded as a member of the Limacinidae Gray, 1847; the hypothesis of its integration to the Peraclididae (Pseudothecosomata) is suggested here but in the meantime it is labelled genus *incertae sedis*.

Concerning the phylogenetic hypotheses we have opted for the 28S but it requires some reservations and further investigations.

Key words

Anatomy, calcareous microstructure, cladistic, distribution, molecular biology, morphology, nomenclature, palaeontology, phylogeny, radula, taxonomy.

Riassunto

Gli Euthecosomata Meisenheimer, 1905 sono Molluschi oloplantonici. Quelli con conchiglie a spirale o diritta erano originariamente classificati come Limacinidae Gray, 1847 (*Limacina* Gray, 1847, *Thielea* Strebel, 1908) e Cavolinidae Gray, 1850 - Cavoliniidae Fischer, 1883 (*Creseis* Rang, 1828, *Styliola* Gray, 1850, *Hyalocylis* Fol, 1875, *Cuvierina* Boas, 1885, *Clio* Linnaeus, 1767, *Diacria* Gray, 1847, *Cavolinia* Abdlgard, 1791, *Diacavolinia* Spoel, 1987). In una analisi cladistica successiva, da quando è stato osservato per la prima volta un cambiamento in quest'ultima famiglia, i generi con conchiglie conica *Creseis*, *Styliola* e *Hyalocylis* sono stati tutti classificati come Creseidae Rampal, 1973. Per verificare quest'ultimo risultato e per aggiornare la tassonomia di tutti gli Euthecosomata, è stato necessario proseguire ulteriormente questo studio in collaborazione con biologi molecolari.

Sulla base dei dati COI i Limacinidae sono polifiletici, i Cavoliniidae risultano poli- o parafiletici da analisi Bayesane o maximum likelihood, rispettivamente, i Creseidae sono polifiletici con entrambi i metodi. Sulla base dei dati 28S diverse famiglie tradizionali non sono monofiletiche. Nella cladogenesi i Limanicidae e i Creseidae sono parafiletici, i Cavoliniidae sono monofiletici. Sulla base dei dati COI, le specie di conchiglie diritte potrebbero probabilmente apparire due volte indipendentemente. Tuttavia il 28S non ha supportato questo scenario ma ha mostrato un'elevata congruenza con i dati morfologici e paleontologici per la risoluzione dei nodi profondi (Corse et al. 2013).

Alla luce di queste nuove intuizioni, è stata proposta una nuova tassonomia dettagliata di questo clade (Rampal, 2017). I Limacinidae sono stati suddivisi in tre famiglie: Limacinidae Gray, 1847, Heliconoididae n. fam. e Thieleidae n. fam. La famiglia Creseidae Rampal, 1973 è stata convalidata con due generi: *Creseis* Rang, 1828 e *Boasia* – precedentemente – sottogenere di *Creseis* (Dall, 1889). *Styliola* e *Hyalocylis* sono *incertae sedis*. I Cavoliniidae Gray, 1850 sono stati suddivisi in quattro sottofamiglie: Cuvierininae Spoel, 1967, Cliinae Jeffreys, 1869, Diacriinae n. subfam. Rampal, 2017 e Cavoliniinae Gray, 1850. I Cre-

seidae Rampal, 1973 e i Cavoliniidae Gray, 1850 appartengono al Cavolinioidea Gray, 1850. Il rango della maggior parte delle specie è stato confermato. I seguenti generi sono stati proposti o ristabiliti: *Telodiacria* n. gen. (Rampal, 2017), *Hyalaea* de Blainville, 1821, *Boasia* Dall, 1889. Il fossile *Vaginella* Daudin, 1800 è stato collocato nei Cuvierininae. Il fossile *Altaspiratella* Korobkov, 1966 non è più considerato come membro di Limacinidae Gray, 1847; l'ipotesi della sua integrazione ai Peraclididae (Pseudothecosomata) è qui suggerita ma nel frattempo è etichettato come genere *incertae sedis*.
Per quanto riguarda le ipotesi filogenetiche abbiamo optato per il 28S ma ciò richiede alcune riserve e ulteriori indagini.

Parole chiave
Anatomia, microstruttura calcarea, cladistica, distribuzione, biologia molecolare, morfologia, nomenclatura, paleontologia, filogenesi, radula, tassonomia.

Introduction

Between the Thanetian (the Latest Paleocene)-Ypresian (Early Eocene) (Watelet & Lefèvre, 1885; Hodgkinson et al., 1992), when the Euthecosomata first appeared, and the Pliocene, two distinct morphotypes with coiled and straight shells diversified. The chronology and shape of the fossils recorded, along with phylogenetic findings, suggest that their adaptation to a planktonic environment took place several stages. First the appearance of swimming organs in the spiral shell populations followed the acquisition and optimisation of straight shells which evolved successively from conical to cylindrical, pyramidal and globular. The spiral and straight shell species were classified as Limacinidae Gray, 1847 and Cavolinidae Gray, 1850 respectively. In a cladistical study (Rampal, 1973), the Cavoliniidae was subdivided into two families: Cavoliniidae Gray, 1850 s. str. and Creseidae Rampal, 1973. The addition of our recent molecular analyses allowed a taxonomic review of all the Euthecosomata. Limacinidae Gray, 1847, Creseidae Rampal, 1973 and Cavoliniidae Gray, 1850 have been redefined. The systematic rank of several species has been validated. Two alternative phylogenetic hypotheses are discussed, as to whether the emergence of the straight shelled Euthecosomata was a single or two-fold event. Palaeontological data giving valuable insights on these results were compared with the molecular data in order to estimate the divergence times and also trace the phenotypic variations which have occurd with time.

Material and methods

The specimens used in the present molecular analyses were mainly collected during the Circum-global TARA Oceans mission (2009-2012), which 68 stations were examined. Specimens were also collected during the following others missions in the Caribbean waters of Mexico and Belize (Eastern Coast of the Yucatan) (January 2007): 16°14′N-21°30′N) / 86°59 W′-88°22′ during the ECOSUR cruise (Chetunal Mexico by Dr R. Gasca) in collaboration with the National Oceanic Athmospheric Administration, in the Caribbean Sea (Virgin Islands), and on the CRER Missions, National Oceanic Athmospheric Administration, Ship: NOAA R/V Nancy Foster; Cruise NF 08 05 (March 2008) and Cruise NF 09 03 (April 2009): 17°25′N-18°55′N / 62°28′W-65°14′W. Pacific Ocean, French Polynesia, Ahe Lagoon, mission FED (October 2008): 14° 49′S-14° 45′S / 146° 35′W-146° 33′W). In the Western Mediterranean Sea, Ship headed by the Oceanologic Center in Marseille (September 2009): 43°06′N-05°22′E. Only some coordinates (longitudes and latitudes) corresponding to specimens collected for positive molecular analyses during the TARA Oceans mission.
The molecular analyses were based on two sets of data: the mitochondrial Cytochrome Oxydase I gene, COI data and data set (with and without noisy sites) and the Large Subunit of ribosomal RNA 28S molecular data and gene data set (with and without noisy sites). The support values (0 to 1) give the posterior probability in the Bayesian tree, while the values (0 to 100) are the Maximum Likelihood bootstrap values. Supplementary molecular data from genebanks and the Bar Coding of Life Database have been used in the case of singular genes (Corse et al., 2013, Tabl. 2). We also used an integrative approach to estimate the divergence times based on the distribution of pairwise genetic distances (Corse et al., 2013). The estimated taxa emergence periods are given in million of years.
The cladistic analyses also included specimens collected during some oceanographic missions conducted by N.O.:Thor, (1910); Dana (1921; 1930), Président-Théodore-Tissier (1957; 1958); Shoyo-Maru (1959); Thalassa (1961; 1963; 1969; 1977); Argonaut (1965), Jean-Charcot (1966; 1979; 1981); Ariadne (1966); Magga Dan (1966-1967); Coriolis (1967; 1969); Korotneff (1970; 1971); La Coquille (1971); Marion-Dufresne (1981; 1982; 1986); Missions Cyclone VI (1967), Caride 4 (1969) (00°00′-05° 22′S, 169°57′-152°32′ W).
The cladistic analysis was based on 54 variables: shell (19), parapodia-footlobe (7), head (3), pallial system (10), gill (1), alimentary system (7), genital system (6), nervous system (1); modality: presence/absence and orderly qualitative data. The matrix is available in PLOS /ONE. org Table. 1&2 (Corse et al., 2013). The cladistical analysis of morphlogical data is available in PLOS/ONE (fig. 2). (Corse et al., 2013). The original phylogenetic trees are available in PLOS/ONE (COI: figs 3, 4; 28S: figs 5, 6). In this manuscript are only used schematic phylogenetic trees (**Figs 16-19**). This study also included a comparative morphological analysis of the radula and the shells' micro-architectural structure (Microscopes

Wild M5 and M10, Scanning Electron Microscope). A first previous exhaustive synonymic lists can be found in the studies by Spoel (1967) quoted in the present references.

Abbreviations

a, apical angle; H, height; L, length; T, thickness; W, width; MA, millions years.
ICZN, INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE.

Results

Systematics

Two orders Thecosomata de Blainville, 1824 and Gymnosomata de Blainville, 1824 (clades according to Bouchet & Rocroi, 2017) belong to Mollusca, Gastropoda, Euopisthobranchia (Wägele et al., 2013). They were classifed together as Pteropoda Cuvier, 1804 and subsequently no longer held to be monophyletic orders related to Cephalaspidea and Anaspidea respectively (Boas, 1886; Pelseneer, 1888; Meisenheimer, 1905; Morton, 1958; Spoel, 1967; Salvini-Plawen, 1970). Therefore, although the term Pteropoda was officially rejected, it often continued to be accepted (Hoffman, 1939; Odhner, 1939).
Now it is supported by molecular analyses: a new clade have been identified including Thecosomata, Gymnosomata and Anaspidea (Dayrat et al., 2001) or including Thecosomata and Gymnosomata (Jennings et al., 2010). According to Klussmann-Kolb & Dinapoli (2006) there is 'revival of Pteropoda'.

Thecosomata de Blainville, 1824

s/O Euthecosomata Meisenheimer, 1905: two parapodia, no proboscis.
1. Spiral calcareous shells with an umbilicus (but no columella).
2. Straight calcareous shells.

s/O Pseudothecosomata Meisenheimer, 1905: a parapodial disc and a proboscis.
1. Spiral calcareous shells with a columella (but no ombilicus): Peraclididae Tesch, 1913.
2. Straight amino-acid pseudoconchs: Cymbuliidae Cantraine, 1841.
3. Without any shell: Desmopteridae Chun, 1889.

Euthecosomata Meisenheimer, 1905 (Spiral shelled Euthecosomata)

Palaeontological summary

Among the earliest known spiral shelled Euthecosomata the fossil *Limacina mercinensis* Watelet & Lefèvre, 1885 emerged during the Early Eocene (Ypresian) (56.5 MY). The fossil *Limacina heatherae* Hodgkinson, 1992 is listed under 'Late Paleocene (Thanetian) (58.6 MY)? – Early Eocene?' (Ypresian) (Hodgkinson et al., 1992: 17). Other spiral species emerged during the Early Eocene and between the Lower and Late Eocene (Hodgkinson et al., 1992). The extant species *Heliconoides inflata* (d'Orbigny, 1835) (syn. *Limacina inflata* Gray, 1850) is known since the Miocene and *Thielea helicoides* Strebel, 1908, since the Upper Miocene (Janssen, 2004).
The fossil genus *Skaptotion* Curry, 1965 emerged during the Middle Eocene (Bartonian): the shell is characterized by a tickened apertural margin expanding into a platform. Four species of this genus has been described by Hodgkinson et al. (1992); occurrences: 'Early - Middle ? Eocene, - Middle Eocene, - Middle-late Eocene'. According to Janssen (2003) *Skaptotion* was held to be synonymous with the extant genus *Heliconoides* d'Orbigny, 1835: 'I retain all forms with apertural reinforcements in a single genus (*Heliconoides*)'. In this way the *Heliconoides* emergence is problematic because of the confusion in the discrimination with *Skaptotion*.

Cladistic and molecular analyses **(Figs 16-19)**

The monophyly of the Limacinidae Gray, 1847 is not supported by either cladistic or molecular data.
– Cladistic: paraphyly of the Limacinidae. The first cladogenesis distinguished *Thielea helicoides* (Jeffreys, 1877) from the Limacinidae.
– COI data: polyphyly of the Limacinidae. They did not form a monophyletic group with *Limacina helicina* (Phipps, 1774).
– 28S data: the species of the genus *Limacina* Bosc, 1817 form a monophyletic lineage.
However because of the absence of 28S data resolutions for *Thielea* and *Heliconoides*, the monophyly of the Limacinidae characterised by Rang, 1827 cannot be tested.

Conclusion

All of the spiral Euthecosomata taxa previously belonged into the same family the Limacinidae Gray, 1847, in a single genus *Limacina* (several synonyms). Based on the cladogenesis, on COI molecular analysis (paraphyly or polyphyly) and on the highly specialised *Thielea* and *Heliconoides*, the original Limacinidae Gray, 1847 has been invalidated. It has been suggested a partition into Limacinidae s. str., Heliconoididae and Thieleidae.

Family Limacinidae Gray, 1847
Genus *Limacina* Bosc, 1817
(Figs 1, 5, 6, 12, 16-19)

Diagnosis

A spiral shell with characteristic H (H/ W =0.6-1.8) and apical angle (a =55°-140°); an ombilicus; a dorsal pallial cavity; oviparity.

Type species: *Clio helicina* Phipps, 1774: 195.

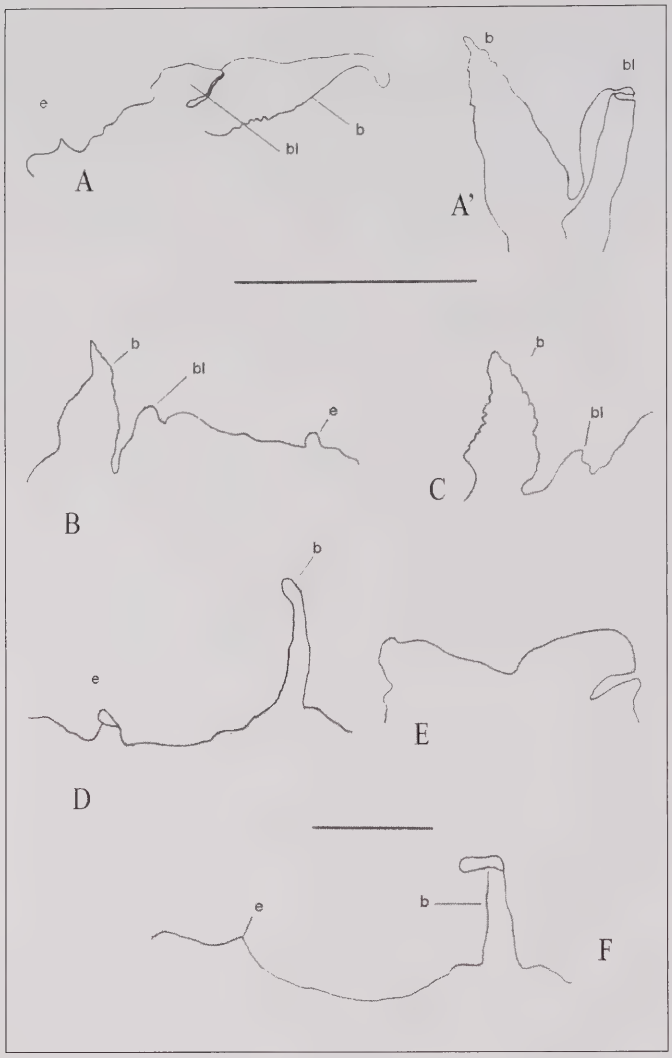


Fig. 1. Anterior pallial appendages. **A, A'**. *Limacina retroversa* (Flemming, 1823) (dorsal view); **B**. *Limacina helicina* (Phipps, 1774) (ventral view); **C.** *Limacina trochiformis* (d'Orbigny, 1836) (ventral view); **D**. *Styliola subula* (Quoy & Gaimard, 1827) (dorsal view); **E**. *Creseis acicula* (Rang, 1828); **F**. *Hyalocylis striata* (Rang, 1828) (dorsal view). b-bl, balancer-basal lobe; e, expansion. Scale: 0.5 mm.

Fig. 1. Appendici palliali anteriori. **A, A'**. *Limacina retroversa* (Flemming, 1823) (vista dorsale); **B**. *Limacina helicina* (Phipps, 1774) (vista ventrale); **C**. *Limacina trochiformis* (d'Orbigny, 1836) (vista ventrale); **D**. *Styliola subula* (Quoy & Gaimard, 1827) (vista dorsale); **E**. *Creseis acicula* (Rang, 1828); **F**. *Hyalocylis striata* (Rang, 1828) (vista dorsale). b-bl, lobo base di bilanciamento; e, espansione. Scala: 0,5 mm.

Species

Limacina bulimoides (d'Orbigny, 1836), *L. helicina* (Phipps, 1774), *L. lesueurii* (d'Orbigny, 1836), *L. retroversa* (Flemming, 1823), *L. trochiformis* (d'Orbigny, 1836).

Material examined

TARA Oceans mission (2009-2012): 674 *Limacina bulimoides* (34°93'S, 17°93E); 172 *L. lesueurii* (53°98'E, 16°95'S; 34°93'S, 17°93'E); 1487 *L. trochiformis* (16°14'N, 86° 59'W; 21°30'N, 88°22'W); 865 *L. helicina* and 169 *L. retroversa* (Antarctic).
TARA mission in the Western Mediterranean Sea, the Caribbean Sea and the South Atlantic Ocean: 88 Limacinidae.

Definition

The species are fairly small except for *L. helicina. L. bulimoides*: W =1-1.7 mm, H =3.5 mm, H/W =2, a =55°; *L. lesueurii*: W =1.3-1.5 mm, H =1.0, H/W =0.7, a =125°; *L. trochiformis*: W =1 mm, H = 1.1 mm, H/W =1.1, a =90°; *L. retroversa*: W =2.4-2.6 mm, H =4.2 mm, H/W =1.6, a =55°-60°; *L. helicina*: L =4-6 mm, H =2.8-4.2 mm, H/W =0.7, a =120°-140° (Rampal, 2011).

There is a variably narrow umbilic and no columella. Presence of an operculum. The superficial micro-ornaments are visible only under Scanning Electron Microscopy (**Fig. 6. A**). The peristome has a thin edge. The calcareous microstructure of the adulte shell is either prismatic and/or crossed-lamellar (**Fig. 9**) (Be et al., 1972; Rampal, 1972; 1974; 1975, Fig. 9; Richter, 1976; Glaçon et al., 1994). The microstructure of *Limacina retroversa* apex is helicoidal (**Fig. 6. F**).
The two thin parapodia each consist of a single lobe but *L. helicina* and *L. retroversa* also show a tentacular lobe on the dorsal edge. There is no proboscis; there is a thin cephalic lobe and asymmetrical rhinophores. The mouth and parapodia are positioned at a similar level, as occurs in the other Euthecosomata. The pallial cavity is dorsal. The anterior margin of the mantle is lined by a single fringe carrying some frontal appendages (Rampal, 1975): a balancer with a basal lobe (sometimes with a beak-like gutter-shaped appearance) and a small expansion (**Fig. 1. A-C**). The pallial gland includes a single layer of parallelepipedic cells on the anterior edge (a second layer in the middle gland in *L. trochiformis*), and a region containing multi-lobed prismatic cells area (**Fig. 5. A**). The intestine includes a single loop; there is multilamellar jaw. The median and lateral radular teeth are clearly visible and highly differentiated (Vayssière, 1915; Spoel, 1967).

Cladistic and molecular analyses (Figs 16-19)

– Cladistic: the first cladogenesis established the paraphyly of the Limacinidae. The genus *Limacina* itself consists of two paraphyletic subgroups: 1. *Limacina helicina, L. retroversa* (tentacular parapodial lobe); 2. *L. lesueurii, L. bulimoides, L. trochiformis.*
– COI data: polyphyly. Breakdown of Limacinidae into subgroups. *L. helicina* is the sister group to the straight Euthecosomata *Hyalocylis.*
– COI data set: *L. helicina* is the sister group to the Pseudothecosomata.
– 28S data: *L. helicina* forms a paraphyletic assemblage with *L. lesueurii, L. trochiformis* and *L. bulimoides.*
There are discrepancies between the various analyses as far as *L. helicina'* position on the various genetic trees is concerned. It is difficult to account more fully for the results because too few data are current available on this species

Conclusion

Because of the lack of congruence between the various gene trees drawn up on *L. helicina*, this species cannot be positioned with respect to the other species. Likewise the fact that too few data are available on *L. bulimoides, L. lesueurii* and *L. trochiformis*, along with the confusion around *L. helicina* makes it impossible to reach any clear-cut conclusions as to whether these species belong to the Limacinidae. These results simply give an initial insight into the classification of this family.

Distribution

In the circumglobal TARA Oceans samples *Limacina trochiformis, L. bulimoides, L. lesueurii* are widely spread across all the oceans, from temperate to tropical zones. *L. bulimoides* is rare. In the Mediterranean Sea, whereas *L. trochiformis* abunds in the South Western and Eastern Mediterranean sea; *L. lesueurii* has rarely been detected anywhere, and only in the Alboran Sea: it serves as a marker showing the presence of the Atlantic current (Rampal, 1965a; 1970a; 1975). *L. helicina* and *L. retroversa* are bipolar psychrophiletic organisms. In the Arctic and Antarctic, *L. helicina* have been specific differentiation (Hunt et al., 2010).
Relatively little is known so far about the diurnal bathymetric levels of the Limacinidae (Rampal, 1966, 1967).

Fossil genus *Altaspiratella* Korobkov, 1966
Incertae sedis

Type species: *Physa elongatoidea* (Aldrich, 1887).

Altaspiratella: Early Eocene (56.5 MY)-Middle Eocene (Lutetian) (46 MY) (Hodgkinson, et al., 1992, text - figs 1, 3). *Altaspiratella* belongs to the Limacinidae Gray, 1847) (Hodgkinson et al., 1992; Janssen et al. 2013).
The genus Limacina 'have a wide umbilicus or, if narrow, very deep. In some species the apertural border is regularly rounded' (Spoel, 1967).
One particulary striking feature which distinguishes *Altaspiratella* from the Limacinidae is the absence of the umbilicus and the presence of a twisted columella ending in an abapical rostrum with a narrow columella membrane (Hodgkinson et al., 1992). 'The columella itself is thickened and shows a distinct torsion in such a way that looking into the shell's interior is possible by a straight adapical view; the apertural margin is widened and internally reinforced with a rather solid ridge connected with the thickened columella' (Cahuzac & Janssen, 2010: 24).
Peracle Forbes, 1844 (Peraclididae Tesch, 1913; spiral Pseudothecosomata) is characterized by a twisted columella (there is no umbilicus) and a rostrum. The latest morphological knowledge tends to support the idea that removal of *Altaspiratella* should be removed from the Limacinidae and be integrated to the *Peracle* lineage. This integration into the Pseudothecosomata is chronologically plausible because it is subsequent to the divergence between Euthecosomata and Pseudothecosomata; we have estimated that this first event took place around 59.1 MY (Paleocene: Thanetian) (Corse et al., 2013).
Altaspiratella started in the Early Eocene (Ypresian) 56.5 MY. Extinction: Middle Eocene (Lutetian) 46 MY. The *Altaspiratella* lineage which disappeard 46 MY ago seems to reappeared with the genus *Peracle* during the Oligocene (Chattian) 29.3 MY. It is entended to test the integration of *Altaspiratella* into the *Pseudothecosomata* using the integrative approach to estimate the divergence times. In the meantime it has been proposed to label *Altaspiratella* a genus *incertae sedis.*
A similar scenario was put forward to explain the relation between *Prehyalocylis* Korobkov, 1962 and the extant species *Hyalocylis* Fol, 1875 (see below).

Family Heliconoididae Rampal, 2017
Genus *Heliconoides* d'Orbigny, 1835
(Figs 6, 12, 16-17)

Diagnosis

A coiled shell with an apex pushing into the last worl of the shell; apical angle a = (nearly) 180°; an umbilicus; a thin and sharp edged peristome; often dorsal rib (s); a dorsal pallial cavity; a prostate; pseudoviviparity.

Type species: *Atlanta* (*Heliconoides*) *inflata* d'Orbigny, 1835: 174

Species

Heliconoides inflata (d'Orbigny, 1835).
The genus was subsequently designated *Heliconoides* d'Orbigny, 1835 and named *Heliconoides inflatus* (d'Orbigny, 1835) by (Herrmannssen, 1846: 514).' That generic name may be a nomen oblitum (Rules, 1961) but is

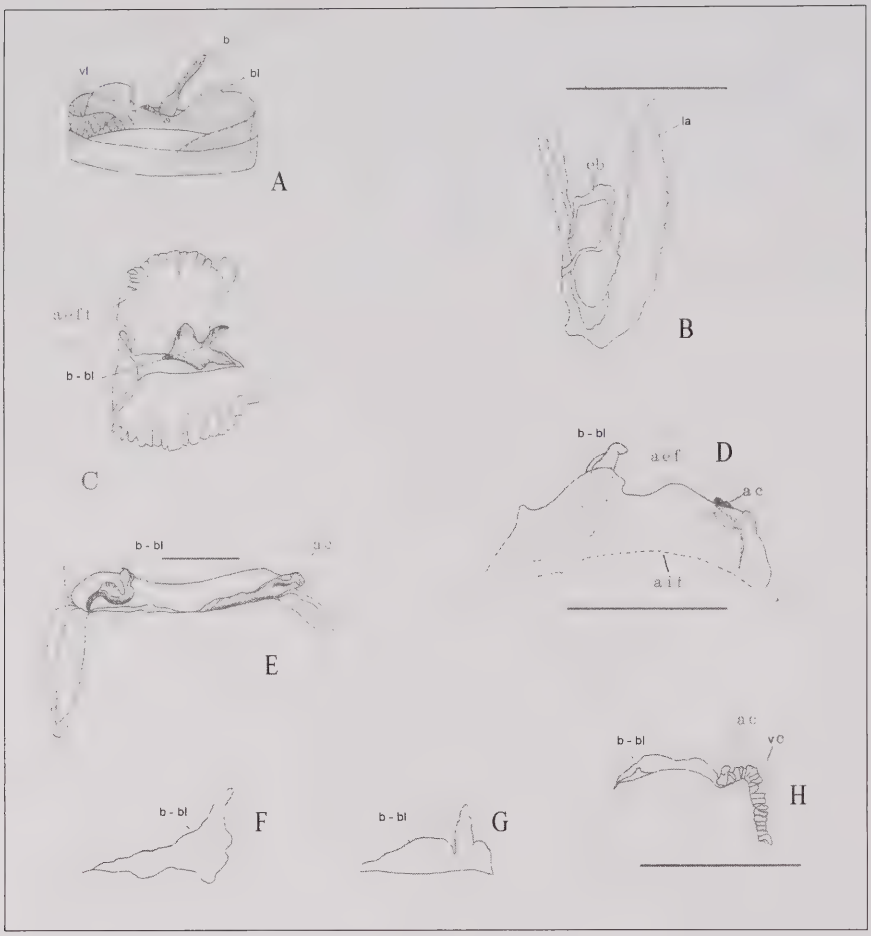


Fig. 2. Anterior pallial appendages (ventral view, except indication). **A**. *Thielea helicoides* (Jeffreys, 1877) (oral view schema); **B.** *Hyalaea cuspidata* (Bosc, 1802); **C**. *Clio pyramidata* Linnaeus, 1767 (folded asymetric fringe); **D**. *Cuvierina columnella* (Rang, 1827); **E**. *Diacria trispinosa* (de Blainville, 1821); **F**. *Clio polita* (Pelseneer, 1888); **G**. *Clio pyramidata* Linnaeus, 1767; **H**. *Telodiacria quadridentata* (de Blainville, 1821) Rampal, 2017. ac, calypter-like appendage; aef, aif, antero-ventral external and internal fringes; aeff, folded antero-externe fringe; b-bl, balancer-basal lobe; eb, bilobed expansion; la, lateral appendage; vc, vacuolized cells; vl, ventral lobe. Scale: 0.5 mm.

Fig. 2. Appendici palliali anteriori (vista ventrale, tranne indicazione). **A**. *Thielea helicoides* (Jeffreys, 1877) (schema di visualizzazione orale); **B**. *Hyalaea cuspidata* (Bosc, 1802); **C**. *Clio pyramidata* Linneo, 1767 (frangia asimmetrica ripiegata); **D**. *Cuvierina columnella* (Rang, 1827); **E**. *Diacria trispinosa* (de Blainville, 1821); **F**. *Clio polita* (Pelseneer, 1888); **G**. *Clio pyramidata* Linneo, 1767; **H**. *Telodiacria quadridentata* (de Blainville, 1821). Rampal, 2017. ac, appendice simile al calittore; aef, aif, aif, frange esterne ed interne antero-ventrali; aeff, frangia antero-esterna ripiegata; b-bl, lobo basale bilanciatore; eb, espansione bilobata; la, appendice laterale; vc, cellule vacuolizzate; vl, lobo ventrale. Scala: 0,5 mm.

otherwise valid' (Curry, 1965: 361). It was used since Janssen (2003).
Heliconoides inflata emerged during the Miocene.

Material examined

TARA Oceans mission (2009-2012): 3432 specimens (36° 21'N, 14° 30'E; 06° 03'N, 73°89'E; 16° 95'S, 53°98'E; 13° 07'S, 47°00'E; 34°93'S, 17°93'E; 09° 66'S, 09°25'W; 34°31'S, 47°59'W; 13°42'S, 96° 56' W; 03° 57'N, 154° 27'W; 12°26'N, 113°67'W; 29°73'N, 79° 67'34°84'N,74° 64'W).
Western Mediterranean Sea, Caribbean Sea (Yucatan; Virgin Islands), Pacific Ocean: 92 specimens.

Definition

Heliconoides inflata is characterized by a planispiral shell with an involute apex pusch into the last voluminous third whorl; W =1.2 mm, H =0.4 mm; H/W =0.3 (**Fig. 12**). There is an opeculum (Rampal, 1964). The calcareous (aragonitic) microstructure of the shell is prismatic (Rampal, 1975, figs 9A-D); near the apex the microstructure is helicoidal (Glaçon et al., 1994). It shows an oval projecting peristome with a thin sharp edge 'peristome fortement saillant…bouche à bords très minces et tranchants' (d'Orbigny, 1835: 175); T =3.5-6 µm (**Fig. 6. A-E**). A long way behind the margin of the sharp peristome, on half of the last whorl, there is a dorsal rib 'une large bande très hyaline terminée en croix près de l'orifice' (Vayssière, 1915, figs 153-155). 'The shell walls above and below the belt are extremely fragile and usually broken' (Cahuzac & Janssen, 2010: 33; pl. 7, figs10-12; pl. 8, fig. 1); nevertheless the other *Heliconoides* drawed by these authors have tickened apertural margins (pl. 6, figs 1-5, figs 6, 7; pl. 7, figs 1-8; pl. 9, figs 1-7): confusion text / figures.
Spoel (1967, fig. 18A) clearly described that the rib consists of one or two oblique ribs on the half of the last whorl, prolonged by a narrow longitudinal rib 'the rostrum' which ends near the pointed peristome. Sometimes only a rectilinear fairly short, variably thickened rib is present (Spoel, 1967, fig. 17B).
Sometimes there is no rib at all: a 'coquille lisse' (d'Orbigny, 1835: 175; 1836, pl. 12, figs 16-19).
The fossils *Heliconoides tertiaria* (Tate, 1887) and *H. linneensis* Janssen, 2008 also have a dorsal rib running parallel to the thin peristome margin, a long way behind this peristome but there is no rostrum; 'the shell in front of this rim is very fragile and broken in practically all specimens' (Cahuzac & Janssen, 2010: pl. 8, figs 2-4; pl. 10 figs 1-3).
The calcareous fibres of the ribs show a chaotic structure on the external surface and a fairly prismatic structure on the internal face (**Fig. 6. D**). The prismatic or crossed-lamellar structure of the aperture wall is similar to that observed in rest of the teloconch (**Fig. 6. B, C**) but thinner. This area has been compared to a glassy

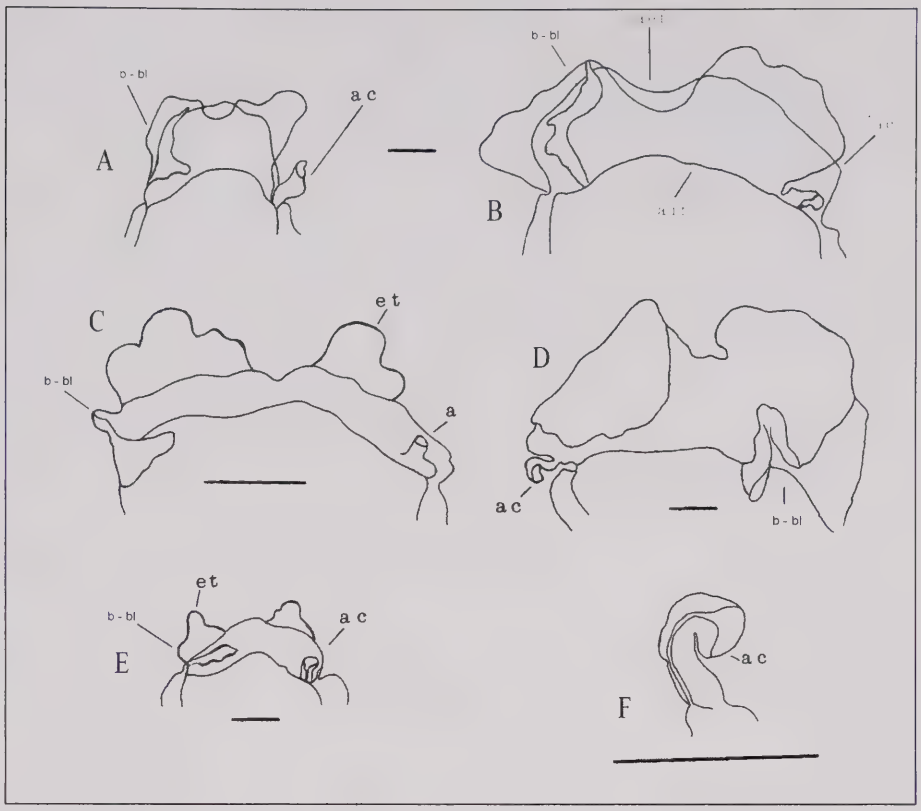


Fig. 3. Anterior pallial appendages (ventral view). **A**. *Cavolinia gibbosa* (d'Orbigny, 1834); **B**. *Cavolinia uncinata* (Rang, 1829); **C**. *Diacavolinia longirostris* Spoel, 1987; **D**. *Cavolinia tridentata* (Niebuhr, 1775); **E**. *Cavolinia globulosa* (Gray, 1850); **F**. *Cavolinia inflexa* (Lesueur, 1813). ac, calypter-like appendage; aef et aif, antero-external and internal fringes; b-bl, balancer-basal lobe; et, trilobed expansion. Scale: 0.5 mm.

Fig. 3. Appendici palliali anteriori (vista ventrale). **A**. *Cavolinia gibbosa* (d'Orbigny, 1834); **B**. *Cavolinia uncinata* (Rang, 1829); **C**. *Diacavolinia longirostris* Spoel, 1987; **D**. *Cavolinia tridentata* (Niebuhr, 1775); **E**. *Cavolinia globulosa* (Gray, 1850); **F**. *Cavolinia inflexa* (Lesueur, 1813). ac, appendice simile a quella di un calice; aef et aif, antero-esterno e frange interne; b-bl, lobo di base del bilanciatore; et, espansione trilobata. Scala: 0,5 mm.

membrane (Rang, 1828) resembling a 'columellar membrane' (Spoel, 1967).

The genital system differs from that observed in all the spiral Euthecosomata and there is pseudoviviparity. Firstly there is no albumin and mucus gland and no penis, but there is a prostate where the spermatophores develop, which is directly connected to the hermaphrodite gland. Secondly, the embryos are attached inside the posterior pallial cavity where they begin to develop; veligers with a shell forming a single sinistral whorl are released together into the plankton (Lalli & Wells, 1973; Wells, 1976) in a sack-like egg capsule (Bandel & Hemleben, 1995).

Molecular analyses (Figs 16, 17)

– COI data and data set: *Heliconoides inflata* and the Limacinidae are not monophyletic. It is the sister group to *Thielea helicoides*; they are the sister group to the Cavolinioidea (not including *Hyalocylis* Fol, 1875, *Cavolinia* Abildgaard, 1791 and *Diacavolinia* Spoel, 1987).

– COI: *Heliconoides inflata* is the sister group to *Creseis* Rang, 1828 (Jennings et al., 2010).

– 28S mol. data: the dotted line corresponds to the topological position of *Heliconoides inflata* obtained when the corresponding sequence is added into the 28S data set; this species shows a very hight rate of substitution. The relation between *Heliconoides inflata* and the other spiral species cannot be clarified.

Conclusion

All of the present highly specific results support a separation of *Heliconoides inflata* from the other extant spiral Euthecosomata in a new family. The highly specific morphological, anatomical, biological (pseudoviviparity) and molecular characteristics confirm its new position. The presence of two distinct lineages (1.00/100) in the Mediterranean and in the Caribbean Sea suggests the existence of different molecular geographically isolated species. Our present molecular analyses make out four several geographical species in the *inflata* group: Atlanto-Mediterranean, Indo-Pacific, South Eastern Atlantic and North Indian species entity; this last is only a little different to the Atlantic entity (one base) but COI confirms his difference (unpublished data). They give evidence to a clade with several species. This pattern was already observed in the other marine organisms.

Nomenclature

The fossil genus *Skaptotion* Curry, 1965 emerged during the Eocene (Bartonian): it has 'apertural margins tickened and expanded into a platform'. Janssen (2003) considered this genus as synonymous to the genus *Heliconoides* d'Orbigny, 1835: 'I retain all forms with an apertural reinforcement in a single genus *Heliconoides*'. However *Heliconoides* has a thin apertural margin that differs quite significantly from *Skaptotion* (see above). This confusion is notably problematic for the palaeontological emergence data. The comparison between these two species needs an integrative approach to the divergence times'estimation.

Distribution

The specimens of the *inflata* group (including many dis-

tinct geographical taxa) collected in the circum-global TARA Oceans samples, have a circum-global distribution (except polar and boreal area); frequence: 75% of the samples; abondance: *inflata* accounted for about 50% of the spiral Euthecosomata; maximum abundance in the Central Pacific Ocean.
This species have a diurnal bathymetric range. The populations which are generally meso-infrapelagic, show daily variations as well as seasonal patterns of migrations (corresponding to the laying period) during which they tend to be epipelagic (Rampal 1964; 1966; 1967; 1975: 371-379).

Family Thieleidae Rampal, 2017
Genus *Thielea* Strebel, 1908
(Figs 2, 5, 7, 12. G, 16, 17)

Diagnosis

A spiral shell with a not very conspicuous apex: apical angle =125°; an umbilicus; a cephalic lobe; a lateral pallial cavity; aplacental viviparity.

Type species: *Limacina helicoides* Jeffreys, 1877: 338.

Species

Thielea helicoides (Jeffreys, 1877).
A relatively recent spiral species which emerged during the Upper Miocene (Tortonian) (Janssen, 2004).

Material examined

Data from Genbank and Life Database BarCoding (Corse et al., 2013).

Coriolis (1967, 1969): the mission Caride IV and Cyclone VI (00°00′, 169°57′E; 01°14′N, 169°49′E; 00°03N, 152°32′E):

Definition

Thielea helicoides can be distinguish morphologically, anatomically as well as ecologically from the others spiral species. Size: W =10.5 mm, H / W =0.9, a =125°. The genus has a thick shell and a very big last whorl. 'The inner aperture margin is curved outwards, a trace of a rostrum is seen with a small columellar membrane like structure (**Fig. 12**) wich is bigger in the Atlantic specimens than in the Pacific ones' (Spoel, 1967). An umbilicus was found to occur in most specimens (Spoel, 1967). The aragonitic microstructure of the shell shows a fairly crossed-lamellar pattern (Rampal, 1975, fig. 9F). The soft parts are brown, the thick and folded parapodia look like a pseudo-parapodal disc and the posterior foot lobe is relatively small. There is a well developed cephalic lobe and a lateral pallial cavity. The anterior mantle border is membraneous, resembling a double fringe, in which the internal layer carry well developed, specialised anterior appendages: a balancer with a basal lobe as well as a ventral lobe (**Fig. 2. A**). These appendages were described by Bonnevie (1913) and Tesch (1946) as a 'gill', similar (but not homologous) to a ctenidium, and as a 'ventral body lobe' in a medio-ventral position. The pallial gland includes an anterior area with a few layers of prismatic multilobed cells and a large area of transversally elongated parallelepipedic cells except in the middle part of the gland where these cells run parallel to the antero-posterior axis (**Fig. 5. B**). The intestine is double-looped.
The median and lateral radular teeth are poorly differ-

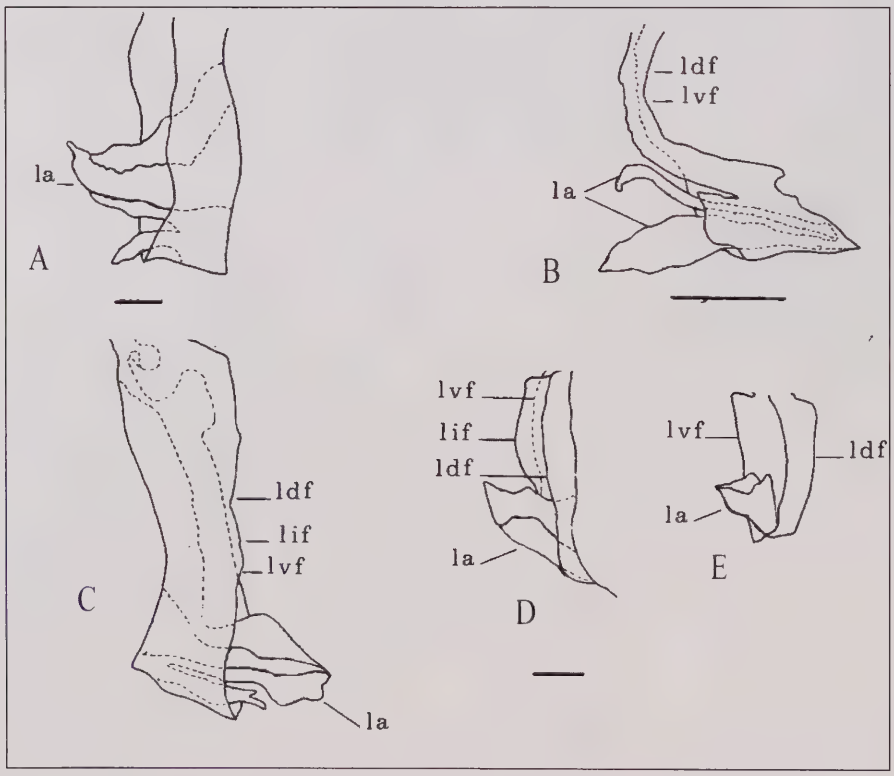


Fig 4. Lateral pallial appendages (dorsal view, except indication). **A**. *Cavolinia gibbosa* (d'Orbigny, 1834); **B**. *Diacavolinia longirostris* (Spoel, 1987); **C**. *Cavolinia tridentata* (Niebuhr, 1775) (ventral view); **D**. *Cavolinia uncinata* (Rang, 1829); **E**. *Cavolinia globulosa* (Gray, 1850). ldf, lif, lvf latero-dorsal, lateral interne and latero-ventral fringe; la, lateral appendage. Scale: 0.5 mm.

Fig 4. Appendici palliali laterali (vista dorsale, tranne indicazione). **A**. *Cavolinia gibbosa* (d'Orbigny, 1834); **B**. *Diacavolinia longirostris* (Spoel, 1987); **C**. *Cavolinia tridentata* (Niebuhr, 1775) (vista ventrale); **D**. *Cavolinia uncinata* (Rang, 1829); **E**. *Cavolinia globulosa* (Gray, 1850). ldf, lif, lvf latero-dorsale, interna laterale e frangia latero-ventrale; la, appendice laterale. Scala: 0,5 mm.

entiated (Vayssière, 1915; Spoel, 1967) and show little variety in term of their shape and size (a noteworth difference in comparision with the teeth present in the other Euthecosomata); the denticles are poorly developed and irregular (**Fig. 7. A, A'**). Another remarkable feature of *Thielea helicoides* is its mode of reproduction: aplacental viviparity (embryos are kept inside the mucus gland). This characteristic is unique among the spiral Euthecosomata (Wells, 1978).

Cladistic and molecular analyses (Figs. 16, 17)

– Cladistic: the first cladogenesis differentiated *Thielea helicoides* from the other Euthecosomata. It is the sister group to all the Euthecosomata.
– COI data and data set: *Thielea helicoides* is not monophyletic with the Limacinidae; it is the sister group to *Heliconoides inflata*; *Thielea* + *Heliconoides* are not monophyletic with the Limacinidae. Together they are the sister group to the straight Euthecosomata (not including the Cavoliniinae Gray, 1850 and *Hyalocylis*.
– 28S: Lack of resolution for *Thielea*.

Conclusion

Both cladistic and COI analyses have shown that *Thielea helicoides* constitutes a separate entity among the other spiral Euthecosomata and confirm that *Thielea helicoides* should be removed from the Limacinidae Gray, 1847. The anatomical (see above), biological (aplacental viviparity), ecological (bathypelagic) and molecular COI data, show that *Thielea helicoides* is distinct from the other spiral Euthecosomata and confim the validity of the new family Thieleidae (Rampal, 1975).
The morphological data are more complexe: presence of an umbilicus in most specimens (ex. Euthecosomata) and trace of a rostrum with a columellar membrane-like structure (ex. Pseudothecosomata); the parapodia look like a pseudo-parapodial disc (Pseudothecosomata) (see above). Interestly there is the discrepency between the recent apparition and the fact that it display some complexe plesiomorphic characteristics of a possible common spiral benthic ancestor?
These findings suggest the occurrence of an evolutionary reversion (Corse et al., 2013). It would be worth performing a further analysis using an integrative approach to estimate the divergence times in order to reach a better understanding of the evolution of this genus.

Distribution

This bathypelagic species can be found at all the latitudes of the Atlantic Ocean, and some rare occurrences have also been observed in the South-Western Pacific Ocean (unpublished data).

Euthecosomata Meisenheimer, 1905
(Straight shelled Euthecosomata)
Superfamily Cavolinioidea (Gray, 1850)

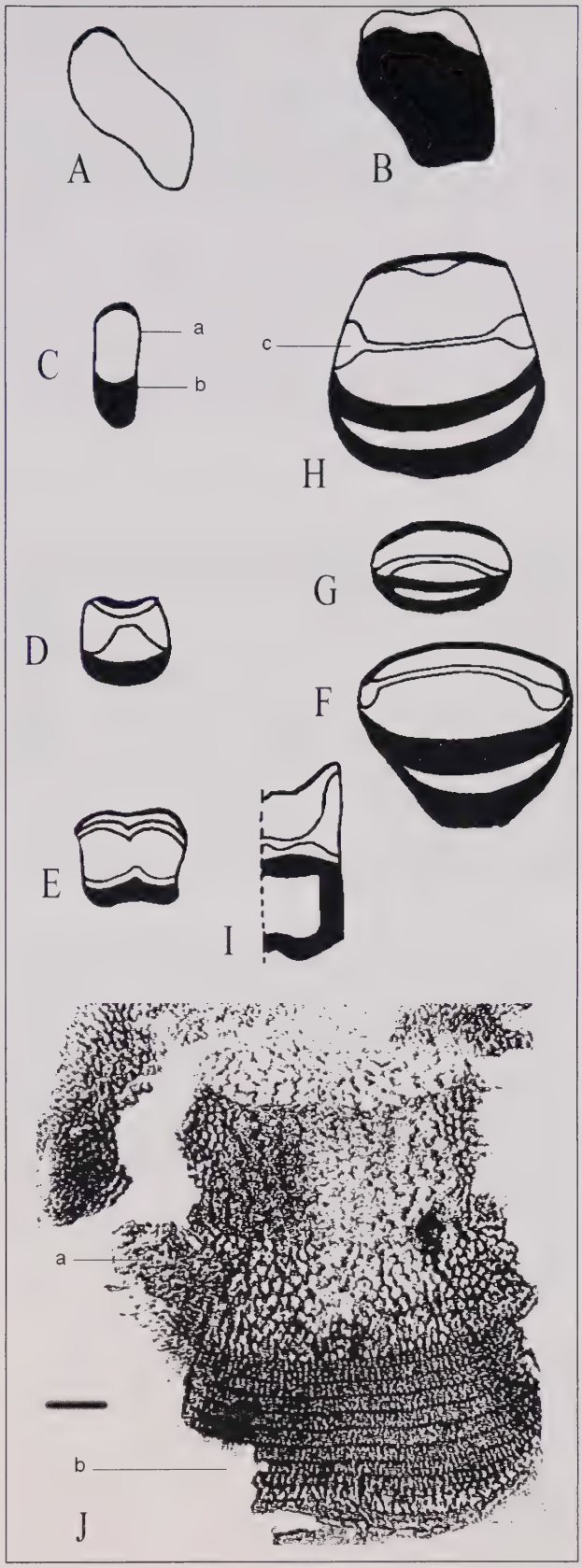


Fig. 5. Pallial gland: A-I (schemas): **A**. *Limacina* Bosc, 1817; **B**. *Thielea* Strebel, 1908; **C**. *Creseis* Rang, 1828; **D**. *Hyalocylis* Fol, 1875; **E**. *Styliola* Gray, 1850; **F**. *Clio* Linnaeus, 1767; **G**. *Diacria* Gray, 1847; **H**. *Cavolinia* Abildgaard, 1791; **I**. *Cuvierina* Boas, 1886. **J**. (SEM microphotograph): *Creseis virgula*. a, prismatic cells; b, parallelepipedic cells; c, dumbbell-shaped prismatic cells area. Scale: 0.1 mm.

Fig. 5. Ghiandola palliale: A-I (schema): **A**. *Limacina* Bosc, 1817; **B**. *Thielea* Strebel, 1908; **C**. *Creseis* Rang, 1828; **D**. *Hyalocylis* Fol, 1875; **E**. *Styliola* Gray, 1850; **F**. *Clio* Linnaeus, 1767; **G**. *Diacria* Gray, 1847; **H**. *Cavolinia* Abildgaard, 1791; **I**. *Cuvierina* Boas, 1886. **J**. (microfotografia al SEM): *Creseis virgula*. a, cellule prismatiche; b, cellule a parallelepipedo; c, area delle cellule prismatiche a forma di manubrio. Scala: 0,1 mm.

Genera

Creseis Rang, 1828, ***Boasia*** Dall, 1889, *Styliola* Gray, 1850, *Hyalocylis* Fol, 1875, *Cuvierina* Boas, 1886, *Clio* Linné, 1767, ***Hyalaea*** de Blainville, 1821, *Diacria* Gray, 1847, ***Telodiacria*** Rampal, 2017, *Cavolinia* Abildgaard, 1791 and *Diacavolinia* Spoel, 1987.

This superfamily resulted from the second significant diversification of the straight Euthecosomata.
The transition from a spiral to a straight shell involves deep and important morphological and anatomical changes: the unwinding of the visceral mass; a 180° twist of the trunk relative to the head; the pallial cavity becames ventral (Boas, 1886) – latero-ventral in *Clio polita* – and the anterior appendages were reversed.
The spiral shelled Euthecosomata have prismatic or crossed lamellar calcareous microfibres. The straight shelled Euthecosomata have helicoidal calcareous microfibres (Be et al., 1972; Rampal, 1972, 1973, 1974, 1975; Curry & Rampal, 1979; Glaçon et al., 1994): it is proposed an hypothetic impact of the macrounwending over the microfibres (Rampal, 1973, 1975).
The first perfectly straight shell to appear is conic. The third main diversifying event, the further optimisation into a more complex apomorphic shell occured progressively late.

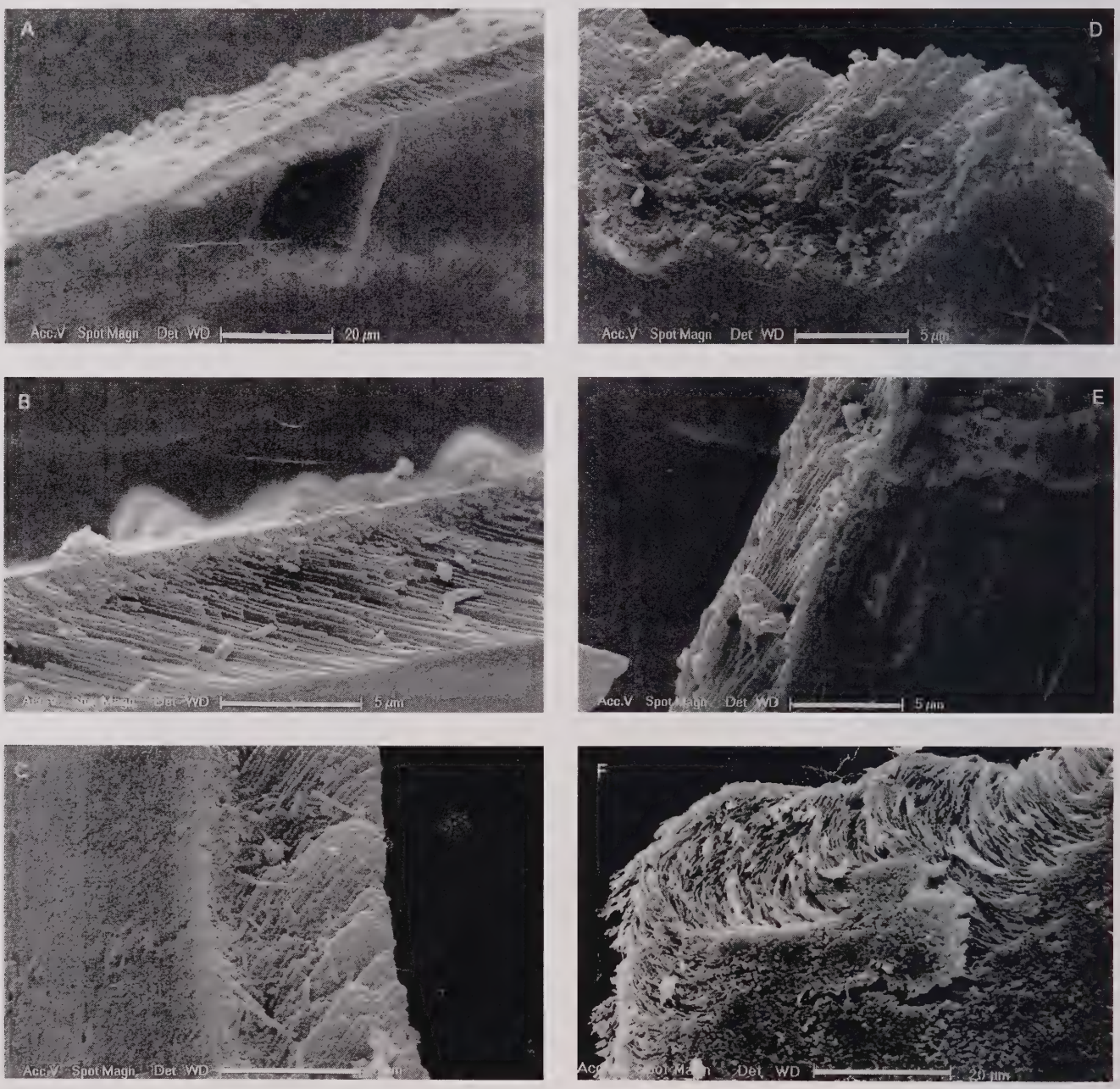


Fig. 6. Calcareous microstructure of the shell: transversal section (SEM microphotographs). **A-C**. *Heliconoides inflata* (d'Orbigny, 1835) without rostrum: **A**. median peristome margin; **B, C**. apical and ombilical peristome margin; **D, E**. *Heliconoides inflata* with rostrum: **D**. rostrum; **E**. peristome margin. **F**. *Limacina retroversa* (Flemming, 1823), apical section.

Fig. 6. Microstruttura calcarea della conchiglia: sezione transversale (microfotografie al SEM). **A-C**. *Heliconoides inflata* (d'Orbigny, 1835) senza rostro: **A**. margine mediano del peristoma; **B, C**. margine del peristoma apicale and ombilicale; **D, E**. *Heliconoides inflata* con rostro: **D**. rostro; **E**. margine del peristoma. **F**. *Limacina retroversa* (Flemming, 1823), sezione apicale.

1. All of the straight Euthecosomata belong to the Cavolinioidea (Gray, 1850).
2. Based on the latest cladistical analyses *Creseis, Styliola* and *Hyalocylis* were removed from this superfamily and placed in the new family Creseidae characterized by a conical shell and some similar characteristic of the pallial complex (Rampal, 1973).
3. Cladistic and molecular analyses have confirmed the validity of this definition of the Creseidae but only limited in the case of *Creseis* and *Boasia* (previously subgenus of *Creseis*); *Styliola* and *Hyalocylis* are still *incertae sedis*.
4. Among the other straight Cavolinioidea Gray, 1850 there is a lack of congruence among the molecular data: COI analyses did not support their monophyly but cladistic and 28S molecular analyses (1.00/65) showed the monophyly of the Cavoliniidae (Gray, 1850) (Corse et al., 2013). Athough this lack of congruence and the necessity about the need to new molcular data based on cladistic and 28S molecular data, it is proposed to subdivise this family into 4 taxa at subfamily level: Cuvierininae, Cliinae, Diacriinae n. subfam. and Cavoliniinae.
This family corresponds to a new radiation event since it broke away from the ancestral conical teloconch to form a more apomorphic teloconch characterized by a dorso-ventral depression, a lateral ridge followed by lateral slits and then a protective lip over the peristome. The times at which the various lineages diverge have been corroborated by the paleontological data (although approximatively concordant in the case of *Clio*).

Superfamily Cavolinioidea (Gray, 1850)
Family Creseidae Rampal, 1973
(Figs 1, 5, 12, 16-19)

Diagnosis

A straight or dorsally curved conical shell; a circular cross-section; a smooth or striated shell; a single anterior fringe on the pallial cavity; parapodia single-lobed but the presence of a little dorsal tentacular lobe; two areas of parallelepipedic cells present in the pallial gland.

Genera: *Creseis* Rang, 1828: 316 and *Boasia* Dall, 1889: 84

Genus ***Creseis*** Rang, 1828: 316

Type species: *Cleodora* (*Creseis*) *virgula* Rang, 1828: 316.

Species

Creseis virgula (Rang, 1828: 316), *C. acicula* (Rang, 1828: 318), *C. conica* Eschscholtz, 1829: 19.

Genus ***Boasia*** Dall, 1889: 84

Type species: *Cleodora chierchiae* Boas, 1886: 202.
Species (ICZN Article 51B: new combination) ***Boasia chierchiae*** (Boas, 1886) Rampal, 2017.
Syn. *Creseis* (*Boasia*) *chierchiae* Dall, 1889; *Creseis chierchiae* Meisenheimer, 1905.

Material examined

TARA Oceans mission (2009-2012): 924 Creseidae. (16°95′S, 53°98′E; 14°59′N, 69°98′E): 342 *Creseis acicula* (35°45′N, 14°15′E): 292 *C. conica*; (73°89′N, 06°03′E): 154 *C. virgula*; 14°59′N, 69°98′E; 06°03′N, 73°89′E): 136 *Boasia chierchiae*.
In the Western Mediterranean Sea, the Caribbean Sea (Yucatan; the Virgin Islands), the Pacific Ocean and the South Atlantic Ocean: 26 Creseidae.

Palaeontological summary

The Creseidae were the first straight Euthecosomata to emerge during the Early Eocene (Ypresian), Middle Eocene (Bartonian) and Early Oligocene. The perfectly straight genus *Creseis* emerged during the Middle Eocene (Bartonian) (41-38 MY) concurrently with the uncoiled fossils *Euchilotheca* Fischer, 1883, *Cheilospicata* Hodgkinson, 1992, *Camptoceratops* Wenz, 1923, *Bovicornu* Meyer, 1887 (Hodgkinson et al., 1992). *Camptoceratops* shows a gradual unwinding of the shell; *Euchilotheca* shows a few features which are not unlike those some taxa: the presence of an internal septum, a platform-like peristome, an oblique peristome and parallel teloconch edges near the peristome. *Cheilospicata* has a conical teloconch and a thickened platform-like peristome which is reminiscent of that observed in the coiled fossil genus *Skaptotion* Curry, 1967. *Bovicornu* has a slightly coiled teloconch: the status of this genus has been challanged by some authors. What is the link between the spiral and straight shapes which have a thickened peristome or between the coiled and straight shell with a thin peristome? These questions still remain to be answered.
Creseis and all of these fossil genera was greatly expanded and diversified during the Tertiary era (Hodgkinson et al., 1992; Cahuzac & Janssen, 2010).

Definition

The shell is thin and variably elongated. *Creseis acicula*, L =20-30 mm; *C. conica conica*, L =5-8 mm; *C. c. falsiparum*, L =6-8 mm; *C. virgula virgula*, L =4-6 mm; *C. v. frontieri*, L =8.0-11.5 mm; *Boasia chierchiae*, L =2.0-3.5 mm. The teloconch is smooth or striated in the case of *Boasia*. It is straight or dorsally curved with a virtually characteristic plurisegmented axis (5 or 6 similar segments for *C. conica*; 3 or 4 uneven segments for *C. virgula*) (Rampal 1985; 2002). It has a circular cross-section, and no lateral ridges. The peristome has thin edges and a circular cross-section (**Fig. 12**). The protoconch can only be clearly seen in *Boasia* (where it is pear-shaped with two constrictions) and in *C. acicula* (which has a protoconch with parallel edges and internally thickened constrictions) (Rampal, 1985). *C. conica* and *C. virgula* have a conical protoconch which tends to flared with a ran-

domly positioned and sized constriction. The parapodia consist of a single lobe but they also have a little dorsal tentacular lobe (which is also present in *Limacina helicina* and *L. retroversa*). The posterior footlobe is fairly small. Like the other Cavolinioidea, the Creseidae have a radula with very different median and lateral teeth and a multilobed jaw (Vayssière, 1915; Spoel, 1967). The pallial cavity is ventral and its margin, which is lined with a single fringe (Rampal, 1975), bears the poorly differentiated front pallial appendages (**Fig. 1. E**). The pallial gland is composed of two areas of parallelepipedic cells (a single-layered one on the anterior margin and a multi-layered one located more posteriorly); these two areas are separated by an area composed of prismatic cells (**Fig. 5. C**).

Cladistic and molecular analyses (Figs 16-19)

In both cladistic and phylogenetic analyses the Creseidae are monophyletic (not including *Hyalocylis* and *Styliola*). In COI gene topology both gene trees are congruent concerning the relationship between lineage inside the Creseidae with 3 distinct lineages: *Boasia, Creseis acicula, C. virgula-C. conica.*
Boasia chierchiae appeared as the sister-group to all the other Creseidae.
– Cladistic: the Creseidae are the sister group to all the other Cavolinioidea.
– COI data (1.00/83) and 28S (1.00/100): the Creseidae are monophyletic.
– COI data (1.00/) and data set (0.94/): they are also the sister group to the Cavolinioidae (not including *Hyalocylis* and the Cavoliniinae Gray, 1850)
– 28S (0.99/78 and 1.00/90): they are the sister group to the Cavoliniidae Gray, 1850.
– COI (1.00/ 99, 1.00/ 100), 28S (0.95/93, 0.97/96): *Creseis conica* and *C. virgula* are sister group.
– 28S (1.00/100): *C. acicula - Boasia chierchiae* are the sister group to *Creseis conica - C. virgula.*
– COI (1.00/100, 1.00/99), 28S (0.97/95): *C. conica* and *C. virgula* have a specific rank.
– COI (1.00/91, 0.99/86): *Boasia chierchiae* is the sister group to all the *Creseis.*
– 28S (1.00/96, 1.00/93): *Boasia chierchiae* is the sister group to *Creseis acicula. Boasia chierchiae - Creseis acicula* are the sister group to *C. conica-C. virgula* (1.00/100).
These analyses also show distinct lineages. *Boasia chierchiae*: 28S (1.00/100, 1.00/90). *Creseis acicula*: COI (1.00/99, 1.00/98); 28S (1.00/93, 1.00/99). *Creseis virgula*: COI (1.00/93); 28S (0.96/97).

Conclusion

These findings support the existence of the synapomorphic Creseidae. The conical teloconch of this clade corresponds to the ancestral plesiomorphic state of the Cavolinioidea. These data also confirm the species rank of the four species previously reinstated on the basis of cladistical analyses (Rampal, 1985; 2002).

Each species comprises several lineages which have been found to occur in various circumglobal localities. This supports the existence of several species-groups in each species.

Creseis Rang, 1828.

– *Creseis virgula* (Rang, 1828: 316) (**Fig. 12. J-K**): *C. virgula virgula* (Rang, 1828), *C. v. frontieri* Rampal, 2002.
– *Creseis conica* Escholtz, 1829 (**Fig. 12. H-I**): *C. c. conica* Escholtz, 1829, *C. c. falsiparum* Rampal, 2002. No substantial regional variation was detected among Atlantic specimens of *C. conica* (Jennings et al., 2010).
– *Creseis acicula* (Rang, 1828: 318) (**Fig. 12. L-L'**). (see below Nomenclature).
C. acicula shows a very stable needle-like phenotype on the world-wide scale; the specimens collected in various localities can be said to be taxa of the cryptic species of the *acicula* group. Recent molecular studies (Corse et al., 2013), have shown that the phylogenetical distances among *C. acicula* (10%) are far greater than in the case of *C. conica* and *C. virgula* (2%): *C. acicula* forms a phenotypically homogeneous polyspecific *acicula* group comprising distinct species rather than infraspecific taxa. The subspecific *C. acicula clava* can therefore be excluded. Affinities have been observed between specimens originating from the Gulf of Aden and the South-Western Indian Ocean as well as between those from the Western Mediterranean and the Caribbean Sea (unpublidhed data).

Boasia Dall, 1889: 84

Boasia chierchiae (Boas, 1886) Rampal, 2017
(Fig. 12. M-M')

Boasia has been perfectly described by monotypy. The molecular analyses show that this species is a member of the Creseidae. The idea that it may constitute a new generic level is a plausible hypothesis. It is morphologically different to the other Creseidae and the number of the diploid chromosomes is different (Zarnik 1911, in Spoel (1967). In both cladistic and COI phylogenetic *Boasia chierchiae* appeared as the sister-group to all the other Creseidae.
Specimens with a smooth or fairly smooth shell were described in the North Mozambique Channel (Frontier, 1963; 1965). According to this author, the ringed form is the most neritic and the smooth or almost smooth specimens sometimes occur beyond the continental rise; these two phenotypes give an example of the polymorphism of a single species (Frontier, 1963; 1965). In the Northern Indian Ocean and the Red Sea, the large majority of specimens observed had only two or three striae (Almoggi-Labin A., 1882. Rampal, 1985). These phenotypes may be linked to *Creseis bulgia* (Saktivel, 1974), which has been identified in the Northern Indian Ocean. Unfortunately, the available data so far do not suffice to be able to establish the systematic levels of the various *Boasia chierchiae* phenotypes.

Nomenclature

– Rang, 1828 described *Cleodora (Creseis) clava* var. *acicula*.
– d'Orbigny, 1834 named this species *Creseis aciculata* (synonym *clava*).
– Souleyet, 1852 proposed *C. acicula* var. *clava*.
– Rampal, 1985 proposed *C. acicula acicula* and *C. a. clava*.
– Janssen, 2005 restored *C. clava*: 'this species is given prirority'.
– WoRMS (2013), data base Janssen (2012): *C. clava* was accepted and *C. acicula* was rejected.
– Rampal (05.01.2017: 23) restored *C. acicula*; *C. clava*, nomen oblitum, was rejected.
– Rampal, 07.12.2017: gave *C. acicula* precedence in a submission to ICZN for confirmation.
– ICZN, 20.02.2018: 'case 3758 has been archived'. The case should therefore be withdrawn and rewritten as a note in a malacological work or as part of any published work that fulfils the relevant section of Article 24 of the code. This message has been archived'.
– Bulletin of Zoological Nomenclature 75 (31 may 2018) ISSN 2057-0570. Notice of new Applications to the Commission cases 3753-3772: 'The following new applications have been received since the last Notice of New Application, was published in the Bulletin (vol. 74, p. 54, 31 august 2017). Under Art. 82 of the code, the prevailing usage of names in the applications is to be maintened until the Commission's ruling on the application (as opinion) have been published Case 3758 *Creseis acicula* (Rang, 1828) substituted for *C. clava* (Rang, 1828): Jeannine Rampal (Mollusca, Gastropoda, Thecosomata, Euthecosomata)'.
– Janssen (Basteria 18.11.2018) gave *C. acicula* precedence 'ICZN ruling is decisive here'.
This declaration of the first *acicula* precedence by Janssen was based on unfounded or erroneous arguments:
1. misapplication of the ICZN ruling: according to ICZN article 23. 9.1.2, *C. clava* is nomen oblitum. According to Janssen *C. clava* is not nomen oblitum: if *C. clava* is not nomen oblitum it should obviously be reinstated.
2. Erroneous analyses of 'previous data: Rampal (2017: 23) used *C. acicula* 'because it has been almost universally adopted since Souleyet (1852); *C. clava* was nomen oblitum'.
Souleyet, erroneous named first reviser, is out of the question in this decision. My opinion is based on the characteristics of *C. acicula* which is in keeping with ICZN article 23.9.1.2 as regards the reversal of precedence. In prevaling usage *C. acicula* was used as valid during the last century, ever since Souleyet (1852) in about 130 works, and it has also been used in at least 25 works published by at least 10 authors during the last uimmediatly preceding 50 years, and encompassing a span of not less than 10 years'.
From 1828 to 1844 a few authors named *C. clava*: Rang & Ferussac (1830: 261), Deshayes & Edwards (1836: 433), Cantraine (1841: 32), Forbes (1844: 132) and later, Issel (1869: 32), apart from a few subsequent isolated citations. Consequently contrary to the Janssen's opinion *C. clava* has not been used as a valid taxon repeatedly after 1899.

Distribution

In the circum-global TARA Oceans samples *Creseis acicula*, *C. conica*, *C. virgula* and *Boasia chierchiae*, account for 37%, 31%, 17% and 15% of the Creseidae respectively. The *acicula* group has a circum-global habitat since it has frequently been found in all the oceans (40°N-40°S) where it is sometimes very abundant. *Creseis conica* occurs the least frequently of all these species in all the area studied. *Creseis virgula*, the most thermophile *Creseis*, is both frequent and abundant in the tropical areas. *Boasia chierchiae* is a typically Indo-Pacific species; it abonds in the South Red Sea during the winter monsoon (Rampal, 1990). However I have identified two specimens in the Caribbean Sea which may possibly have been pre-isthmatic relics.

Superfamily Cavolinioidea Gray, 1850
Genus *Styliola* Gray, 1850
(Figs 1, 5, 7, 12, 18, 19)
Incertae sedis

Diagnosis

A conical shell; an oblique longitudinal groove; a circular cross-section; a single anterior pallial fringe; a pallial gland with two parallelepipedic cells' area.

Type species: *Cleodora subula* Quoy & Gaimard, 1827: 233.

Species ***Styliola subula***
(Quoy & Gaimard, 1827)

This genus may have been present since the Late Oligocene.

Material examined

TARA Oceans mission (2009-2012): (16°95'S, 53°58'E): 173 specimens Western Mediteranean Sea, Caribbean Sea (Yucatan; Virgin Islands): 73 specimens.

Definition

Styliola subula has a conical teloconch (with a circular cross-section. L =7.0-13.0 mm. An oblique longitudinal groove extends from the peristome across the anterior two thirds of the dorsal side, and forms a thin pointed overhang. The peristome itself has thin edges. The pear-shaped protoconch is comparable to but not exactly similar to that observed in *Cuvierina* (**Fig. 12. N'**). The parapodia are relatively short in comparison with the length of the body. The posterior footlobe is semi-circular like that of *Diacria* and *Clio*. The single fringe on the anterior margin of the mantle bears a long balancer and a short expansion (**Fig. 1. D**). In the pallial gland the separating line between the two areas of parallelepipedic cells and

the area of prismatic cells is ondulate (**Fig. 5. E**). The radular teeth have a long and thin cuspid and their base is covered with fine denticles (**Fig. 7. C**).

Cladistic and molecular analyses (Figs 16-19)

– Cladistic: *Styliola* is the sister group to *Hyalocylis* and to the Cavoliniidae.
– 28S mol. data (0.83/): it is the sister group to *Hyalaea cuspidata* and to the Cavoliniidae.
– 28S gene data set: it is the sister group to *Hyalaea cuspidata* and to *Cuvierina* and *Clio*.

Conclusion

These findings support the idea that *Styliola* shoud be removed from the Creseidae Rampal, 1973. Based solely on comparison between the ancestral and acquired features of their teloconch, the existence of affinities between *Styliola* and *Cuvierina* do not seem to be substantiated. However, the characteristics of the embryonic development sheds new light on these possible affinities. *Styliola* may be the first rising lineage which developed from a *Cuvierina*-like ancestor and showed the present-day morphological features as long as about 24 MY ago: the conical plesiomorphic teloconch of *Styliola* is reminiscent of the juvenile shell of *Cuvierina* which consists of a comparable protoconch? *Styliola* may be a neotenic form of *Cuvierina*. The embryonic development of *Styliola* stopped at an early stage corresponding to the ancestral conical stage. However, the polytomy of *Styliola-Cuvierina* rules out the possible existence of a link between the two genera; *Styliola* should therefore be regarded as a genus of *incertae sedis*. In the 28S gene data set (1.00/100) only a single species of *Styliola* is present; however the above hypotheses are difficult to substantiate because of the lack of data based on other analyses.

Distribution

In the circum-global TARA Oceans samples: *Styliola subula* accounted for 11% of the Cavolinioidea; it is present in all the oceans (40°N-40°S). It was frequently found in the South-Western and Eastern Mediterranean Sea (Rampal, 1975) and in the Northern Red Sea (Rampal, 1990).

Superfamily Cavolinioidea Gray, 1850
Genus *Hyalocylis* Fol, 1875
(Figs 1, 5, 7, 12, 16-19)
Incertae sedis

Diagnosis

A striated and dorsally curved conical shell; an ellipsoidal cross-section, a deciduous juvenil shell; a single anterior pallial fringe; a pallial gland with two parallelepidedic cells area, and a dumbbell-shaped layer in the prismatic area.

Type species: *Cleodora* (*Creseis*) *striata* Rang, 1828: 315

Species ***Hyalocylis striata*** (Rang, 1828)

The genus *Hyalocylis* is known to be present since the Upper Miocene (Ujihara, 1996). One (or two) extant species (see below) and several fossils species have been described.

Material examined

TARA Oceans mission (2009-2012) (39°53'N, 12°50'E; 35°45'N, 14°15'E): 87 specimens.
Western Mediterranean Sea, Caribbean Sea (Virgin Islands), Pacific Ocean: 12 specimens. (ED mission 2008)
Pacific Ocean, French Polynesia (14°49' S, 146°35'W; 14°45'S, 33°W): 3 singular specimens.

Definition

Hyalocylis striata has a dorso-ventrally depressed conical teloconch with a dorsal curvature, an ellipsoidal cross-section, approximately 30 transversal striae, a peristome with thin edges and no lateral ridges (**Fig. 12**). L =6.0-9.0 mm. The young shell with conical-shaped protoconch is discarded by the adult, where a blunt apex is closed by a septum, resembling what occurs in *Cuvierina* (**Fig. 12. O'**). The two parapodia are very large in comparision with the length of the body. They are rarely folded back into the shell; the ciliated area observed at their base that, again, resembles that present in the *Cuvierina*. The posterior footlobe is greatly reduced. The anterior margin of the mantle is lined with a single fringe as in *Creseis* (Rampal, 1975) and carry a long thin balancer as well as a small triangular expansion (**Fig. 1. F**). The pallial gland resembles that of *Creseis*, although a similar dumbbell-shaped layer to that observed in *Cuvierina*, is to be found in the prismatic zone (**Fig. 5. D**). The radular teeth have a long thin cuspide; the trapezoidal base of the median tooth is covered with long fine denticles (**Fig. 7. D**). Some singular specimens have been found in the Pacific Ocean (Mahe Lagoon) showing dark marks on the edge of the parapodia (**Fig. 11**).

Cladistic and molecular analyses (Figs 16-19)

– Cladistic: *Hyalocylis striata* is the sister group to the Cavolinioidea (not includig *Creseis*).
– COI data set: it is the sister group to all the Cavolinioidea + *Heliconoides inflata* + *Thielea helicoides*.
– COI data: together with *Limacina helicina*, it is the sister group to the Pseudothecosomata.
– 28S mol. data: it is the sister group to *Cuvierina*.
– 28S gene data set: it is the sister group to the Cavolinioidea (not including *Creseis*).
These molecular analyses also show that the singular specimens with dark marks on the parapodia are very

likely to be undergoing speciation. (**Figs 7. E, E', 11**) (COI: 1.00/100; 28S: 1.00/99, 1.00/100).

Conclusion

These cladistic and molecular analyses support the idea that *Hyalocylis* should be removed from Creseidae Rampal, 1973, as also previously concluded in the case of *Styliola* (Rampal, 1975: 118, 119, 122). *Hyalocylis* has only a few features in common with *Creseis*, mostly focusing the conical shell and the pallial complex: there is a single fringe and only two areas containing parallelepipedic cells in the pallial gland. The other traits distinguishing it from Creseidae include a dorso-ventral depression, the presence of a dumbbell-shaped layer of prismatic cells and the shedding of the juveline shell. Based on the 28S data, there are affinities with *Cuvierina*. To summarize, the phylogenetic position of *Hyalocylis* is difficult to ascertain and the data show great instability both between genes (COI, 28S) and with the same gene (Corse et al., 2013). However, its ties with the *Cuvierina* lineage should not be under-estimated. The *Hyalocylis* lineage may have diverged from *Cuvierina* lineage during the Eocene and subsequently acquired its present morphology. Despite the lack of congruence between the results presented in the 28S tree, the hypothesis that *Hyalocylis* and *Cuvierina* may descend from a common lineage cannot be definitively ruled out. Future studies are now required to elucidete this point. Meanwhile it seems to appropriate to label *Hyalocylis* as genus of *incertae sedis*.
This is not the first time, the affinities of *Hyalocylis* have proved to be difficult to assess. According to Meisenheimer (1905) '*Hyalocylix*' originated from *Creseis* before giving rise to *Cuvierina*. Bonnevie (1913) later suggested that *Clio* (*i.e.*, *Clio*, *Creseis*, *Hyalocylis*, and *Styliola*) may have originated from *Clio polita* before evolving into *Cuvierina*. In their molecular analyses of the Opisthobranchia, Klussman-Kolb and Dinapoli (2006), found *Hyalocylis* to be basal to *Cavolinia*, *Diacria*, *Cuvierina* and *Clio*. According to Jennings et al. (2010) 'the Euthecosomata were not monophyletic unless *Hyalocylis striata* and *Limacina helicina* sequences were excluded'.

Distribution

In the circumglobal TARA Oceans samples: *Hyalocylis striata* accounted for 6% of the Cavolinioidea. It has often been found to occur in the inter-tropical zones of the Atlantic and Indo-Pacific Oceans. It is even more abundant and frequent in the Eastern Mediterranean Sea (Rampal, 1970 b; 1975) and present in the Southern Red Sea (Rampal, 1990a). According to Jennings et al. (2010) 'no substantial regional variation was detected among the samples originating from the Atlantic Ocean.

Fossil genus *Praehyalocylis* Korobkov, 1962

Type species: *Praehyalocylis chivensis* Korobkov & Makarova, 1962).

This fossil genus is known to have been present from the Early Eocene onwards (Ypresian, 56.5 MY) (Hodgkinson et al. 1992). The extant genus *Hyalocylis* Fol, 1875 appeared quite recently (6 MY) during the Upper Miocene-Pliocene (Ujihara, 1996). The relationship between the two genera seems to be in contradiction with their morphological differences: *Praehyalocylis* shows a very large conical teloconch with no dorso-ventral depression, a circular cross-section, a very thin abundant transversal pattern of striation (about 80 striae) no dorsal curvature, a persistent juvenile shell and an elongated protoconch with a slight constriction. The idea of integrating *Praehyalocylis* into the *Hyalocylis* lineage was supported in our integrative study on the divergence times reported in Corse et al. (2013). *Praehyalocylis* started fairly early (Middle Eocene) in comparison with the late emergence of *Hyalocylis* (Upper Miocene-Pliocene). It seems likely that the fossil *Praehyalocylis*, which emerged about 50 MY earlier with some plesiomorphic ancestral characteristics, reappeared with *Hyalocylis*, both belong to the same lineage.

Superfamily Cavolinioidea Gray, 1850
Family Cavoliniidae Gray, 1850

Diagnosis

A dorso-ventral depression; a triangular or elliptic cross-section; lateral ridges; a double anterior fringe in the pallial cavity; the pallial gland contains three area with parallelepipedic cells (transitional characterisitics in the case of *Cuvierina*).

Genera: *Cuvierina* Boas, 1886, *Clio* Linné, 1767, ***Hyalaea*** de Blainville, 1821, *Diacria* Gray, 1847, ***Telodiacria*** Rampal, 2017, *Cavolinia* Abildgaard, 1791, *Diacavolinia* Spoel, 1987.

Palaeontological summary

The genus *Cuvierina* emerged during the Middle Eocene (Lutetian). The other genera belonging to the Cavoliniidae Gray, 1850 emerged during the Oligocene but radiated mostly during the Miocene, long after the arrival of the earliest Cavolinioidea. *Clio* emerged during the Lower Oligocene (Rupelian) (35 MY). The other genera appeared between the Lower Miocene and the Pliocene: Fossil *Gamopleura* (Bellardi, 1873) (Chattian-Burdigalian); Fossil *Diacrolinia* Janssen, 1995 (Aquitanian-Langhian); *Cavolinia* (late Langhian); *Diacria* (late Tortonian) (Cahuzac & Janssen, 2010). *Gamopleura* has a *Cavolinia*-like shape: it has a large globular teloconch and noticeable lateral ridges (at times set into a groove); however, contrary to *Cavolinia* there are no lateral slits. The peristome has an ellipsoidal shape *Diacrolinia* resembles *Diacria* in trems of its extremely short juvenile shell (which measures only a few millimetres) ending in a spherical or oval protoconch and its thick-lipped peristome. *Diacavolinia* Spoel, 1987 emerged during the Miocene-Pliocene.

Definition

The parapodia and the posterior foot lobe are variably highly developed among the genera belonging to this family. There is a double fringe on the anterior pallial cavity (Rampal, 1975); the internal fringe carries highly diversified anterior appendages: a balancer (basal lobe and a calypter-like appendage) (**Figs 2, 3**). *Hyalaea cuspidata, Cavolinia* and *Diacavolinia* have highly developed lateral appendages (**Fig. 4**). The pallial gland is composed of three parallelepipedic cells' areas (a single layered on the anterior margin and two pluri-layers connected laterally). These areas are separated by two areas containing prismatic cells; the anterior one includes a dumbbell-shaped layer (**Fig. 5. F-I**). Depending on the genus, the radula has a median tooth with a pointed triangular or thin cuspid and a variably thick large base, which is covered on both sides with long denticles that can reach up very high on the cuspid (Vayssière, 1915). As the other Euthecosomata the lateral teeth are comma-shaped (**Figs 8-10**).

This clade constituted another significant step in the cladogenesis of the Cavolinioidea. This diversifying event was characterized by an increase in the volume of the teloconch and a dorso-ventral depression. *Cuvierina* was the first to undergo the process of radiation, a transition from the ancestral conical teloconch to an apomorphic cylindrical-subcylindrical teloconch, a dorso-ventrally depression limited to the peristome, a circular transversal section, the absence of lateral ridges, a temporary juvenile conical shell with a pear-shaped protoconch (which is discarded during development) and the apex of the adult teloconch closed by a septum. In the other genera lengthwise lateral ridges determine the dorsal and ventral sides. *Diacria, Telodiacria, Cavolinia* and *Diacavolinia* have open lateral slits linked by closing mechanisms. As the result of the last diversification, the peristome is protected by a dorsal lip; this lip is fairly thin in *Cavolinia* and *Diacavolinia*, and thick in *Diacria* and *Telodiacria*.

Based on the cladistic and molecular analyses the Cavoliniidae Gray, 1850 have been subdivised into four subfamilies: Cuvierininae Spoel, 1967, Cliinae Jeffreys, 1869, Diacriinae Rampal, 2017, Cavoliniinae Gray, 1850.

Superfamily Cavolinioidea Gray, 1850
Family Cavoliniidae Gray, 1850
Subfamily Cuvierininae Spoel, 1967
Genus *Cuvierina* Boas, 1886
(Figs 2, 5, 7, 13, 16-19)

Diagnosis

Cylindrical, subcylindrical teloconch; a bean-shaped peristome; a deciduous conical juvenile shell; two types of superficial micro-ornements of the shell.

Type species: *Cuvieria columnella* (Rang, 1827)

Species: *Cuvierina columnella* (Rang, 1827) (**Fig. 13. B**); *C. urceolaris* (Mörch, 1850) (**Fig. 13. A**); ***C. major*** nomen novum (syn. *Cuvierina. columnella* f. *atlantica* Spoel, 1970; *C. columnella atlantica* Bé et al., 1972; *C. spoeli* Rampal, 2002) (**Fig. 13. C**) (see below); *C. cancapae* Janssen, 2005 (**Fig. 13. D**); *C. pacifica* Janssen, 2005 (**Fig. 13. E**); *C. tsudai* Burridge et al., 2016 (**Fig. 13. F**).

Material examined

TARA Oceans mission (2009-2012): *Cuvierina columnella, C. major* and *C. urceolaris*: (16°95'S, 53°98'E; 29°50'S, 37°99'E; 26°30'S, 110°92'W): 21 specimens.
Caribbean Sea (Yucatan; Virgin Islands): 10 specimens.

Definition

The shell is composed of a cylindrical teloconch and a deciduous conical juvenile shell (**Fig. 13**). The position of the diameter maximum (bulge) is characteristic: d % =D/0.5 L (relative distance from bulge to mid-shell).
Cuvierina columnella: a cylindric shell, L =6.3-7.0 (or 8.0) mm, with the bulge near the middle of the shell, d% =8.3-12; linear micro-ornaments.
C. major: a subcylindric shell, L =7.8 (or 8.8)-10.1 (or 11.1) mm, with the bulge near the apex, d% = 32-34; crossed micro-ornaments.
C. urceolaris: bottle shaped subcylindrical shell, L =5.3 (or 6.0)-6.9 mm, bulge: d% =7-11; crossed micro-ornaments.
C. pacifica: an almost cylindrical shell, L =6.6-8.5 mm, bulge: d% =14-17; micro-ornaments?
C. cancapae: a subcylindric shell, L =7.5-9.3 mm, bulge, d% =9; micro-ornaments?
C. tsudai: an almost cylindrical shell, L =7.2-8.8 mm; bulge, d% =16; micro-ornaments?
– Comment: in the original description *C. c.* f. *atlantica* (*C. major*) was said to be larger than *C. columnella* (Spoel 1970: 120). Whereas according to Janssen (2005) and Burridge et al. (2015; 2016) the larger of the two species is *C. columnella*.

The peristome is bean-shaped (with a dorso-ventral depression). The juvenile conical shell, has a circular cross-section (similar to that of the Creseidae teloconch) with a pear-shaped protoconch wich is only temporary because the juvenile shell is discarded in the course of development. The apex of the adult teloconch is closed by a septum where some remnants of the juvenile shell can sometimes still persist.

The parapodia which are fluffy on both sides are almost as long as the body, the posterior footlobe is greatly reduced. At the base of the parapodia there is a ciliated area ressembling that observed in *Hyalocylis*. The transient organ present at the base of the neck, -called a cervical organ, is thought to play a role during copulation (Vayssière, 1915). The pallial complexe is similar to that observed in the other Cavoliniidae (**Figs 2. D; 5. I**), but differs strikingly from those present in the Creseidae. The median radular tooth is very different from that which occurs in the other Cavolinioidea; it is triangular,

lined with short tight denticles along the entire length and the base is flat and fairly thin (**Fig. 7. B**). The nervous system of Euthecosomata is diversified with a tendency for a ganglia to merge; two particularly noteworthy features of *Cuvierina* are the fact that the pleural ganglia are visible externally and the existence of a second pedal commissura, as occurs in the benthic Gastropoda *Actaeon* (Boas, 1886; Vayssière, 1915; Hoffmann, 1939).

Cladistic and molecular analyses (Figs 16-19)

– Cladistic: the Cuvierininae are monophyletic. They are the sister group to the other Cavolinioidea (not including *Creseis, Boasia, Styliola, Hyalocylis*) (polytomy *Styliola-Cuvierina*).
– COI data and data set (0.93/ and 0.95/): *Cuvierina* is the sister group to *Diacria +Telodiacria, Clio*.
– 28S mol. data (0.97/): *Cuvierina* is the sister group to *Hyalocylis*.
– 28S gene data set (1.00/82) *Cuvierina* is the sister group to *Clio convexa + C. pyramidata*.
– COI data and data set clearly distinguish *C. columnella* from *C. urceolaris* (1.00/100).
– 28S data & gene data set (1.00/100, 1.00/99): distinguish between *C. columnella, C. major* and *C. urceolaris*.

Conclusion

Since there is a lack of congruence between the two 28S molecular data it is difficult to assess the relationships with the other genera. However toward the hypothetical sequence of the morphological evolution of the Euthecosomata, *Cuvierina* obviously play a transitional role in the Cavoliniidae: affinities have previously been described as regards the pallial complex (Rampal, 1973, 1975) but the dorso-ventral depression is only present in the péristome. Molecular clook analyses highlighted a basal position for the Indo-Pacific *C. urceolaris* (Corse et al., 2013). The split between *C. columnella* and *C. urceolaris* is relatively recent (Pliocene). Putting aside *Hyalocylis, Cuvierina* is the sister-group to *Diacria-Telodiacria; Clio* in COI & 28S molecular data suggested the split of the Cuvierininae lineage in 3 species *Cuvierina columnella, C. major, C. urceolaris* although more specimens have to be include before robust statement.
Three species attributed to forma level (Spoel, 1970) were previously instated at species rank: *C. major, C. columnella* and *C. urceolaris* (Rampal, 2002: 212-215) cofirmed by our molecular analyses: 28S mol.data (1.00/100): *Cuvierina urceolaris* is the sister group to *C. columnella* and *C. major*. *C. major* is the sister group to *C. columnella* (Corse et al. 2013, figs 3-6).
C. cancapae and *C. pacifica* have been described in molecular analyses: *C. pacifica* includes two distinct taxa: *C. pacifica N* and *C. pacifica S*. (Burridge et al. 2016, fig. 2). Further molecular analyses have shown that *C. pacifica N* constitutes a distinct species: *C. tsudai* (Burridge et al., 2016: 5, fig. 1 A-I).
Molecular clock analyses have shown that the bottle-shaped Indo-Pacific *C. urceolaris* occupies a basal position: the split between *C. columnella* and *C. urceolaris* was relatively recent (Pliocene) later than the Miocene era suggested by Janssen's (2005). In fact this division into two subgenera (Janssen, 2005) is not supported by either morphologicaly, anatomicaly or molecular clock evidence (Corse et al., 2013). The bottle shaped fossil *C. lura* that appeared early in the Middle Eocene may constitute the original phenotype characteristic of the Indo-Pacific Ocean.
To summarize, the genus *Cuvierina* resulted from the first radiation of the Cavoliniidae, involving a transition from the ancestral conica shell to an apomorphic cylindrical teloconch with a dorso-ventral depression limited to the peristome. The original cylindrical, subcylindrical and bottle-shaped morphotypes have subsisted since the Middle Eocene.

Nomenclature

– Rang (1827: 322-328, pl. 45, figs 1-6) described *Cuvierina columnella*: cylindric shell, L =11mm, d =8.3%, bean shaped peristome and a deciduous juvenille shell. Type locality 'mer des Indes'.
– Spoel (1970: 114, 120, 140) divided this species into a small Indo-Pacific '*C. c.* forma *columnella* (Rang, 1827) and a larger Atlantic forma *C. c.* f. *atlantica* nov. forma'. Under ICZN Articles 15; 45.5.1, the species established with infrasubspecific rank are not available.
– Bé et al., 1972 included the correct *Cuvierina columnella atlantica* in a calcareous shell study. They described *C. c. atlantica* but they illustrated *C. c. columnella:* there is a misidentification.
Under ICZN Articles 49; 69A. *C. c. atlantica* is not available. It cannot be applied to a species which has been wrongly named. In addition, according to ICZN 16.4 and 72 this study is said to be essentially descriptive and according to ICZN Article 16.1 every name published after 1999 including the new replacement name should be explicity presented as being intentionally new: the taxonomical intention had not been specified here.
– Rampal (2002: 212-215, tabl. 1, 2, fig. 1) classified at specific rank these Cuvierininae. Out of respect for the author of a new taxa, the new forma *atlantica* was named *C. spoeli* n. sp. Rampal, 2002.
Under ICZN Article 72 (d) *C. spoeli* is not a new species but a nomen novum: incorrect spelling.
– Janssen (2005: 41, 45, 46, figs 8-11; 2018: 371) described *atlantica* but illustrated *columnella*.
Under ICZN Articles 49; 69A; 70b *C. atlantica* is not available (misidentification); it cannot be retained for the species which has been wrongly named.
Under ICZN Article 18: confusion about the original Spoel's species. The species names are unappropried.

– New point of view
Under ICZN Article 10 (b) a name established with infrasubspecific rank, becames available if it is eleved to a rank of the species-group and takes the date and authorship of its elevation.

– The species rank was attributed by Rampal (2002).
– ICZN Articles 15; 45.5.1; 49; 69A; 70b; 16.4; 72; 16.1; 72 (d) and 18 have made impossible to maintain the *atlantica* terminology (see above).
Therefore *Cuvierina major* nomen novum replaced *Cuvierina atlantica*.

Distribution

In the circum-global TARA Oceans mission the Cuvierininae accounted for 6% of the Cavoliniidae; they to be found between 40°N-40°S. *C. major* and *C. columnella* have the widest distribution of the Cuvierininae.
C. major is most typical for the Atlantic Ocean. It has also been found in the South-Western Indian Ocean and in the Western & Central Pacific Ocean (Spoel, 1970; Rampal, 1990b, 2002).
– *C. major* (in the subtropical zone) and *C. cancapae* (in the equatorial zone) are to be found in the Atlantic Ocean (Burridge et al., 2016).
– *C. columnella* is particularly typical of the Eastern Pacific but it is also found in a larger Indo-Pacific area; it is also to be found in the Atlantic Ocean (Spoel, 1970).
C. major and *C. columnella* has rarely been found in the Mediterranean Sea and restricted to the Alboran Sea where they taken as an indicator to the presence of the Atlantic current (Rampal 1965a; 1970a; 1975).
– *C. urceolaris* is a typically Indo-West Pacific taxon but a few rare occurences have been reported in the North-Eastern Pacific Ocean (Tesch, 1913, 1948).
– *C. tsudai* and C. *pacifica* have been found in the South Pacific Ocean. They are considered endemic of this Ocean (Burridge et al., 2016).

Fossil cuvierininae

The following genera occured during the Eocene: *Cuvierina* Boas, 1886, *Tibiella* Meyer, 1884, *Bucanoides* Hodgkinson, 1992 (Lutetian); *Loxobidens* Hodgkinson, 1992 (late Lutetian) (Hodgkinson et al. 1992). *Ireneia* Janssen, 1995 (Upper Oligocene) (Cahuzac & Janssen, 2010). I would add to this list the genus *Vaginella* Daudin, 1800 (Lower Oligocene) which has been previously suggested to have possible links with the genus *Cuvierina* (Rampal, 1996; 2002).
– *Bucanoides*, *Tibiella* and *Loxobidens* have a cylindrical or cylindrical-subcylindrical teloconch with a central bulge of various sizes and a small depression at the back of the apertural margin. There is no lateral ridge. The peristome is roughly circular or oval and is reinforced in a platform-like structure in *Loxobidens* and *Tibiella* (Hodkinson et al., 1992). The presence/ absence of this platform-like feature, which is also occurs in some Creseidae fossil, is likely to bear systematic significance, as is the case for the coiled shell species having tickened peristome.
– *Vaginella* Daudin, 1800.
Oligocene (Rupelian)-Upper Miocene (Langhian)-(Tortonian) (there was a chronological error in Rampal, 1996: 180; 2002: 215). It was taken to belong to the 'Hyales' family (Souleyet, 1851; 1852.), to the Cavoliniidae (Spoel, 1967, 1970; Cahuzac & Janssen, 2010).
However, close phenotypical affinities between *Vaginella* and *Cuvierina* were previously mentioned (Rampal, 1996: 180; 2002). In *Vaginella* several phenotypical features are strongly reminiscent of *Cuvierina*: a bottle-shaped teloconch with a central bulge, a dorso-ventrally depressed peristome (with an ellipsoïd to semi-circular shape) with a slightly concave ventral edge, a blunt apex ending in a septum, and a circular to sub-oval transverse section depending on the species. Several characteristics reflect the occurrence of a transition between Cuvierininae and Cavoliniinae: the dorso-ventral depression of the teloconch is not very pronounced in *Vaginella* and the lateral ridges are restricted to the third or half length of the teloconch (a dorso-ventral depression and lateral ridges run along the whole length of the teloconch in the Cavoliniinae); there are not slits in *Vaginella*. On the whole, these features suggest the existence of a closer phylogenetic link between *Vaginella* and the Cuvierininae than with the Cavoliniinae. Comparisons between *Cuvierina inflata* (Bellardi, 1873) and *Vaginella depressa* Daudin, 1800 are consistent with this point of view. Further support for the existence of this link is provided by the synonymy wich has occurd between *Vaginella* and *Cuvierina*. In short despite the lack of available anatomical and molecular data, these morphological features strongly suggests the existence of close affinities between *Cuvierina* and *Vaginella*, which is transitional form of the Cuvierininae.
This point of view was partly approved in the case of *Vaginella* and *Ireneia* (Cahuzac & Janssen, 2010: 75). In view of the morphological features of *Ireneia striatocarinata* the latter authors 'would be inclined to accept a common ancestor for *Vaginella* and *Ireneia*'. Finally, given the ontogenetic criterion, they decided to keep *Vaginella* in the Cavoliniidae (Cahuzac & Janssen, 2010: 100; Janssen 2012: 405).
– *Ireneia* Janssen, 1995.
Oligocene (Chattian)-Upper Miocene. *Ireneia* has an elliptic to semi-circular peristome reminiscent of that observed in the Cuvierininae. However, some other features are more distinctive: it has a conical teloconch, reaches a maximum diameter at the level of the peristome and no septum (because of the persistent apex) (Janssen, 1995). As a reminder, *Cuvierina* has a cylindrical or bottle-shaped shell in which the maximum diameter is never at the level of the peristome and the apex which is only temporary, ends in a septum. This suggests that *Ireneia* which appeared fairly late in the lineage seems to be a plesiomorphic sister group to the genus *Cuvierina*.
– *Cuvierina* Boas, 1886
Since its emergence in the Middle Eocene (Lutetian) until the Pliocene, during which most of these species became extinct, the *Cuvierina* genus underwent important diversification. The earliest occurrence, during the Middle Eocene (Lutetian), was *Cuvierina lura* Hodgkinson, 1992, which has a bottle-shaped teloconch. The next occurrence was *C. gutta* Hodgkinson, 1992, during the

Middle Eocene (Bartonian), wihich has a sub-cylindrical shell (Hodgkinson et al., 1992). The subsequent fossil species, which appeared between the Lower and Upper Oligocene, underwent an extensive process of radiation between the Lower and Middle Miocene before becoming practically extinct during the Pliocene (Janssen, 2005). The species are either cylindrical, sub-cylindrical or bottle-shaped.

Janssen (2005) argues that some features of *C. lura* and *C. gutta* such as their early emergence, the absence of micro-ornaments, their small size and the presence of juvenile shell remnants, suggest that they may be Precuvierinidae. This hypothesis is not very convincing for several reasons: these fossils appeared at the same time as the other Cuvierininae fossils (see above), the presence of micro-ornaments is a random characteristic (which has even been mentionned by Janssen himself), and their size is within the range of the other genera dating back to the Middle Eocene (*C. gutta*, L =2.2 mm; *C. lura*, L =1.0 mm; *Bucanoides*, L =2.0-3.0 mm; *Tibiella*, L =3.5-5.2 mm). In addition, very few similar remnants of juvenile shell of the others species including extant ones have been described. *Cuvierina gutta* and *C. lura* therefore meet the same criteria as the other *Cuvierinae*.

Superfamily Cavolinioidea Gray, 1850
Family Cavoliniidae Gray, 1850
Subfamily Cliinae Jeffreys, 1869
(Figs 2, 5, 8, 13, 16-19)

Diagnosis

A total dorso-ventral depression of the triangular teloconch; lateral ridges; a triangular or ellipsoidal cross-section; a semi-circular posterior footlobe.

Genera: *Clio* Linnaeus, 1767 and ***Hyalaea*** de Blainville, 1821 (Rampal, 2017).

Genus *Clio* Linnaeus, 1767: 1094

Type species: *Clio pyramidata* Linnaeus, 1767: 1094.

Species & Subspecies

Clio chaptalii Gray, 1850, *Clio polita* (Pelseneer, 1888), *Clio recurva* (Childern, 1823), *C. pyramidata pyramidata* Linnaeus, 1767, *C. p. lanceolata* (Lesueur, 1813), *C. p. sulcata* (Pfeffer, 1879), *C. p. martensii* (Pfeffer, 1880), *C. convexa* (Boas, 1886), *C. antarctica* Dall, 1908, *C. excisa* Spoel, 1963, *C. piatkowskii* Spoel et al., 1992.

Genus *Hyalaea* de Blainville, 1821: 9

Type species: *Hyalaea cuspidata* Bosc, 1802: 241.

Species

Hyalaea cuspidata Bosc, 1802; syn. *Clio cuspidata* (Bosc, 1802).

Material examined

TARA Oceans mission (2009-2012): (05°99'S, 73°90'E; 16°95'S, 53°98'E; 13°08'S, 46°97'E; 39°89 N, 12°24 E): 79 Cliinae

Mediterranean Sea, Caribbean Sea (Yucatan; Virgin Islands): 15 Cliinae.

Palaeontology

According to palaeontological data, the Cliinae data back to the Lower Oligocene (35 MY), 37.8 MY as established by Corse et al. (2013) using a pairwise genetic distance-based method to estimate the divergence times. *Clio* then underwent considerable diversification at the species or infra-species level during the Middle Miocene (Langhian). Most of the extant taxa appeared during the late Pliocene (Cahuzac & Janssen, 2010).

Definition

The Cliinae have a pyramid-shaped shell, specific lenghs (see **Figs 13. H-Q**) a variably pronounced dorsal curvature and a triangular or ellipsoidal cross-section. They have angular or flat lateral ridges but no lateral slits or closing mechanism. In some species, the shell is transversally striated. The peristome is wide and its dorsal and ventral lips are not curved. There are three longitudinal dorsal ribs which do not occur in *Clio polita*. *Hyalaea cuspidata* have long dorsal and lateral spines. The protoconch is characteristic of these species: *Clio polita* and *Hyalaea cuspidata* both have a spherical protoconch (with a terminal point in the latter (**Fig. 13. H″, I″**), whereas the other Cliinae have an oval protoconch. The posterior footlobe is semi-circular. The pallial cavity is generally ventral but it is medio-lateral in *Clio polita*. The fringe and the appendages on the anterior mantle and the pallial gland are comparable to those observed in the other Cavoliniidae, but they are smaller in *Clio polita*. In the *pyramidata* group the right-hand half of the anterior external fringe of the mantle is folded (**Fig. 2. C**). The median teeth of the radula have various forms; *C. pyramidata* have a trapezoidal-quadrangular base with many long denticles and a thin cuspide (**Fig. 8. A**); *Hyalaea cuspidata* have a triangular base with short denticles and a triangular curved cuspid (**Fig. 8. D**). *Clio polita* also differs from the other Cliinae in that they have a symmetrical nervous system with merged visceral and pedal ganglia (Bonnevie, 1913; Tesch, 1946; Spoel, 1967).

Cladistic and molecular analyses (Figs 16-19)

The cladistic analysis included: *Clio convexa*, *C. recurva*, *C. chaptalii*, *C. pyramidata*, *Hyalaea cuspidata* and *Clio polita*. Unfortunaly the taxonomic sampling and the resolution of the phylogenetic trees required for the molecular analysis were obtained only in the case of *Clio pyramidata*, *C. convexa* and *Hyalaea cuspidata*.

– Cladistic: the Cliinae are monophyletic and they are

the sister group to the Diacriinae n. subfam; *Clio polita* is the sister group to *Clio recurva* and *Clio chaptalii.*
– COI: the Cliinae are monophyletic; *Hyalaea cuspidata.* is the sister group to the new monophyletic clade *Clio pyramidata* + *C. convexa*; the Cliinae are the sister group to *Diacria trispinosa* + *D. major.*
– 28S gene data set: the Cliinae are not monophyletic (in relation to *Hyalaea cuspidata*); *H. cuspidata* is the sister group to *Styliola subula*; they are the sister group to the Cuvierininae and to the other Cliinae.
– 28S mol. data: the Cliinae are not monophyletic; *Hyalaea cuspidata* is the sister group to *Styliola subula* as well as being the sister group to other the Cavoliniidae (except for the Creseidae).
According to Jenning et al. (2010) the COI data show that *Clio recurva* is geneticaly similar in the Eastern and Southern Atlantic Ocean.

Conclusion

The monophyly (COI) or the polyphyly (28S) of the Cliinae was not determined because of the inconsistent position of *Hyalaea cuspidata.*
Clio polita and *Hyalaea cuspidata* stand out very clearly as entities among the Cliinae.

Clio polita (Pelseneer, 1888)
(Fig. 13)

There are too few data available so far in the resolution of the phylogenetic trees to be abble to detect if the species *Clio polita* belongs to a new genus (*Preclio*?). However this bathypelagic species shows some plesiomorphic characteristics such as the medio-lateral pallial cavity (an incomplete twisting of the trunk), short anterior pallial fringes, flat blunt parapodia, a double-looped intestine, a symmetrical nervous system with fused visceral and pedal ganglia, a flattened dorso-ventral teloconch, small lateral ridges and the absence of dorsal ribs. Altough the molecular analyses were incomplete, the morphological, anatomical and ecological characteristics observed suggest that this species carries traces of the Cliinae's common ancestor in a plesiomorphic ancestral state. This bathypelagic species may have emerged recently from an ancient lineage keeping some of its original features. This hypothesis could be tested using the integrative approach to estimate the divergence times, and new molecular data.

Hyalaea cuspidata (Bosc, 1802)
(Figs 2, 5, 13, 16-19)

The molecular analyses suggest the occurrence of a generic break in this species wich was previouly named *Clio cuspidata.* In COI gene tree it was the sister-group to *Clio pyramidata*-C. convexa. On the contrary in the 28S trees this species displayed an inconsistent position. The Cliinae are not monophyletic given this inconsistent position of *Hyalaea cuspidata.* This species also differs from the other Cliinae in terms of several features: the lateral and dorsal spines of the teloconch, the spherical protoconch with a terminal spine, the characteristic unusual intestinal appendage, not to be found in the other Cliinae (Tesch, 1946; Spoel, 1967), one dorsal and two long and retractile lateral appendages, left lateral bilobed expansion (Rampal, 1965b) which might be described as a calypter like appendage (**Fig. 2. B**).
Despite its relative phenotypical stability, different sequences 'were detected in *Hyalaea cuspidata* from one region to another (SE Atlantic vs. Southern Ocean)' (Jennings et al. 2010).

Nomenclature

The species *falcata* Pfeffer, 1880: 96 used to be alternately named *falcata* and *politum* Pelseneer, 1888: 60:
– *Cleodora falcata* (Boas, 1886: 80; Massy, 1920: 204); *Clio falcata* (Meisenheimer 1906: 107; Massy, 1909: 26). *Clio falcatum* (Meisenheimer, 1905b: 422); *Clio* (*Euclio*) *falcata* (Bonnevie, 1913: 21).
– *Balantium politum* Pelseneer, 1888: 60; *Clio* (*Clio*) *polita* (Pelseneer, 1888); *Clio polita* (Tesch, 1903; Meisenheimer, 1905b:20); *Clio* (*Balantium*) *polita* (Johnson, 1934: ·152); *Euclio polita* (Tesch, 1946: 15; Menzies, 1958: 384); *Clio polita* (Spoel, 1967: 75). According to Tesch (1946) 'Meisenheimer (1905b) objected to the use of the name of *polita* on account of it being only a manuscrit designation so the name *falcata* Pfeffer was restored by them'. However since Johnson (1934) the name *C. polita* (Pelseneer, 1888) has been widely adopted.

Distribution

In the circum-global TARA Oceans samples: the Cliinae accounted for 22% of the Cavoliniidae. *Clio convexa* is a characteristically Indo-Pacific member of the Cliinae. A subspecies *Clio convexa cyphosa* Rampal, 2002 was identified in the Red Sea.
The *pyramidata* group is polytypic and polymorphic (Spoel, 1963, 1967, 1969a; Rampal, 1975, 2002). *Clio pyramidata lanceolata* accounted for 62% of the Cliinae collected during the TARA Oceans mission. It has a circum-global pattern of distribution. *C. p. pyramidata* occurs in the border of the range of distribution of *C. p. lanceolata.* In the Southern Atlantic Ocean the representatives of the *pyramidata* group are very variable: *C. p. sulcata*; *C. p. martensii. C. p. antarctica.*
Some taxa have been raised to the species level: *C. convexa, C. antarctica; C. excisa.*
Hyalaea cuspidata is present but not very abundant in all the oceans of the world (it accounted for 11.4% of the Cliinae). It was found during the Tara Oceans mission in the Eastern Mediterranean Sea, the Northern Indian Ocean, the Atlantic Ocean (the Eastern South Atlantic, Central South Atlantic, Western South Atlantic, and Western North Atlantic).
C. recurva and *C. chaptalii* have a discontinuous worldwide distribution.
The bathypelagic species *Clio polita* seems to be characteristic of the Atlantic Ocean.

Superfamily Cavolinioidea Gray, 1850
Family Cavoliniidae Gray, 1850
Subfamily **Diacriinae** Rampal, 2017
(Figs 2, 5, 8, 14, 16-19)

In cladistic data Diacriinae and Cavoliniinae are not monophyletic. They correspond to two distinct lineages.
Diacria Gray, 1847 and ***Telodiacria*** Rampal, 2017 formed a new clade that is the sister group to Clio. *Diacria* is the sister group to the Cliinae and *Telodiacria* is the sister group to *Diacria* + Cliinae.
28S gene tree was congruent with this topology whereas in the COI *Telodiacria* is the sister-group to Diacria + Cliinae. Beyong this incongruency (monophyly or not of Diacriinae) the analyses supported the new genus *Telodiacria* and justify the new subfamily Diacriinae polyphyletic with the Cavoliniinae.
The Diacriinae are known to be present since the Miocene (Tortonian)-Pliocene (Cahuzac & Janssen 2010).

Diagnosis

A variably globular teloconch with lateral ridges and slits; a peristome with a thickened short dorsal lip and a rudimentary closing system; a long juvenile shell (which can be either persistent or deciduous) with flat lateral ridges and a semi-circular posterior footlobe.

Genera: *Diacria* Gray, 1847 and *Telodiacria* Rampal, 2017

Genus *Diacria* Gray, 1847
(Figs 2, 5, 8, 14, 16-19)

Adult and persistent younger shell

Type species: *Hyalaea trispinosa* de Blainville, 1821

Species: *Diacria trispinosa* (de Blainville, 1821), *D. major* (Boas, 1886), *D. rampalae* (syn. *D. rampali*) Dupont, 1979, *D. maculata* Beeker & Spoel, 1988, *D. piccola* Bleeker and Spoel, 1988, *D. gracilis* Rampal, 2002.

Genus *Telodiacria* Rampal, 2017
(Figs 2, 14, 16-19)

Etymology: telo = adult status (the younger shell is deciduous)

Type species: *Diacria quadridentata* de Blainville, 1821.

Species, ICZN Art. 51B, new combination n. comb.: *Telodiacria quadridentata* (de Blainville, 1821) Rampal, 2017; *T. costata* (Pfeffer, 1879) Rampal, 2017; *T. danae* (Spoel, 1968) Rampal, 2017; *T. schmidti* (Spoel, 1971) Rampal, 2017.

Material examined

TARA Oceans mission (2009-2012): 34°93'S, 17°93'E: 58 *Diacria* (mainly young specimens) Caribbean Sea (Yucatan; Virgin Islands): 13 *Diacria*.
TARA Oceans mission (2009-2012): (21°47S, 54°27'E; 16°09'S, 42°83'E; 20°94'S, 35°19'W): 132 *Telodiacria* (mainly young specimens).
Caribbean Sea (Yucatan; Virgin Islands): 31 *Telodiacria*.

Definition

– Genus *Diacria* Gray; 1847
Teloconch + younger shell: L =7.6-11 mm.
A dorso-ventraly flattened teloconch (with an ellipsoidal section) with long lateral spines: L =5.44-8.69 mm; H =2.05-2.91 mm); W (spines) =5.97-11.08 mm. A very long narrow persistent younger shell with flat lateral ridges and a spherical protoconch (**Fig. 14. A-I**). This shell is hyaline and sometimes of a brownish colour. The median radular teeth have a broad short base with short denticules and a curved triangular cuspid (**Fig. 8. E, F**). The *trispinosa* group is polytypic and polymorphic: *Diacria trispinosa trispinosa* (Blainville, 1821), *Diacria trispinosa atlantica* Dupont, 1979 (L =9.66-11mm), *Diacria trispinosa heterocolorata* Rampal, 2002 (L =7.06 mm); *Diacria major* (Boas, 1886) (L teloconch =7. 40-8.69 mm) (the juvenile shell is often discarded); *Diacria rampalae* Dupont, 1979 (L =8.72-10.48 mm); *Diacria maculata* Bleeker and Spoel, 1988; *Diacria piccola* Bleeker and Spoel, 1988; *Diacria gracilis* Rampal, 2002 (L =8.86-10.10 mm) (Rampal, 2002).

– Genus *Telodiacria* Rampal, 2017
The younger shell which has an oval protoconch is deciduous.
Main features: globular hyaline or brown teloconch, no lateral spines, apex closed by a septum. There are three to five variably dorso-longitudinal ribs; the ventral face has transversal striae. The peristome has a thickened dorsal lip with transversal striae; (**Fig. 14. J-M**). Near the lateral fringes of the pallial cavity there is a characteristic region containing vacuolised cells (**Fig. 2. H**).
Telodiacria quadridentata: l =2.5-3.0 mm; a hyaline shell, a tickened peristome sometimes with a brown border; five longitudinal slightly swollen dorsal ribs and some less proeminent transversal striae.
T. costata: L =3.5-4.0 mm; a solid thicker shell; a hyaline sometimes brown shell; five deep long sharp well developed dorsal ribs; clearly prominent transversal striae.
T. danae: L =1.6-1.9 mm; a hyaline shell; 3 swollen fairly short ribs; transversal striae (**Fig. 14. J-M**). In our samples we have never observed *T. erythra* and *T. schmidti*.

Molecular analyses (**Figs 16-19**).

COI & 28S: *Diacria* lineage is monophyletic.
– 28S mol. data (0.97/) and gene data set (1.00/100): *Diacria* is the sister group to *Telodiacria*; they form a monophyletic lineage: *Diacria* belongs to the Diacriinae.
These analyses support the taxonomic rank of three species (there are no genetic sequences available for *Dia-*

cria gracilis). However the relationships between the species were unclear since the topology changes in function of data with or without noisy site).
– 28S data (1.00/100): *D. trispinosa* is the sister group to *D. rampalae* + *D. major*.
– 28S data set (0.99/96): *D. rampalae* is the sister group to *D. trispinosa* + *D. major*
According to Jennings et al. (2010) *Diacria trispinosa* specimens 'from widely separated ocean basins were geneticaly similar (Eastern Atlantic and South Eastern Indian); specimens with 'sequence differences were detected between regions for *Diacria major* (North Western Atlantic vs. South Eastern Indian'
– COI data: 0 sequence: few results were obtained on *Telodiacria* because there were much fewer adult than juvenile specimens.
– COI data set (1.00/94, 1.00/95): *Telodiacria* is monophyletic; one young undetermined specimen is the sister group to *T. quadridentata* and *T. danae*.
– 28S data set: *T. danae* is the sister group to two youg undetermined specimens.

Distribution

In the circum-global TARA Oceans expedition:
– *Diacria* accounted for 16.4% of the Cavoliniidae. *D. trispinosa atlantica*: Nord Atlantic (30°N-60°S). *D. trispinosa trispinosa*: circumglobal (35°N-35°S). (other taxa were certainly assimilated to this species).
D. rampale: circumglobal (20°N-35°S). *D. gracilis*: Western Pacific Ocean. *D. major* has rarely been found in any of the oceans.
– *Telodiacria* (mostly young specimens) accounted for 20.6 % of the Cavoliniidae. *Telodiacria quadridentata* and *T. costata* was collected in the Indo-Pacific area. *T. danae* have a circumglobal distribution. *T. erythra* was observed in the Red Sea and in the Western Indian Ocean; *T. schmidti* was observed in the Eastern Pacific.

Superfamily Cavolinioidea Gray, 1850
Family Cavoliniidae Gray, 1850
Subfamily Cavoliniinae Gray, 1850
(Figs 3, 5, 9, 15-19)

Diagnosis

A fairly globular teloconch with ridges and slits; a long peristome with a curved dorsal lip; a well developed closing system; characteristic dorsal ribs; no juvenile shell; a wide posterior foot lobe.
The Cavoliniinae occur from the Miocene (Langhian) period onwards.

Genera: *Cavolinia* Abildgaard, 1791: 175 and *Diacavolinia* Spoel, 1987. 77.

Genus *Cavolinia* Abildgaard, 1791

Type species: *Cavolinia tridentata* (Niebuhr, 1775)

Species:

– *Gibbosa* group: *Cavolinia gibbosa* (d'Orbigny, 1834), *C. flava* (d'Orbigny, 1834), *C. plana* Meisenheimer, 1905), *C. gibboides* Rampal, 2002.
– *Inflexa* group: *C. inflexa* (Lesueur, 1813) (*C. i. inlexa* and *C. i. Imitans*), *C. labiata* (d'Orbigny, 1834).
– *Tridentata* group is composed of at least nine members: *C. tridentata* (Niebuhr, 1775) and infraspecific taxa: *affinis* (d'Orbigny, 1836), *occidentalis* (Dall, 1908), *Kraussi* (Tesch, 1913), *danae* Spoel, 1968), *dakarensis* Spoel, 1974, *atlantica* Spoel, 1974, *teschi* Spoel, 1974, *bermudensis* Spoel, 1974 (Pfeffer, 1880; Boas, 1886; Schiemenz, 1906; Mac Gowan, 1960; Spoel, 1974; Rampal, 1975).
– *Uncinata* group: *C. uncinata uncinata* (Rang, 1829), *C. uncinata* forma *pulsata* Spoel, 1969; *C. uncinata* forma *roperi* Spoel, 1969.
– *C. globulosa* (Gray, 1850).

Genus *Diacavolinia* Spoel, 1987
(Fig. 15. L)

Type species: *Hyalaea longirostris* de Blainville, 1821.

Species:

Diacavolinia angulosa (Spoel, 1970), *D. strangulata* (Spoel, 1970), *D. longirostris* (Spoel, 1970), *D. limbata* (Spoel, 1970), *D. flexipes* Spoel, 1971, *D. mcgowani* Spoel, 1973.
Sixteen species were described by Spoel et al. (1993), including the following new species: *D. aspina, D. atlantica, D. bandaensis, D. bicornis, D. constricta, D. deblainvillei, D. deshayesi, D. elegans, D. grayi, D. ovalis, D. pacifica, D. robusta, D. souleyeti, D. striata, D. triangulata, D. vanutrechti.*

Material examined

TARA Oceans mission (2009-2012): (14°59'N, 69°98'E; 06°O3'N, 73°89'E; 21°47S, 54°27'E; 16°95'S, 53°98' E; 16°09'S, 42°83'E; 34°93'S, 17°93'E): 63 *Cavolinia* and *Diacavolinia*.
Western Mediterranan Sea, Caribbean Sea (Yucatan, Virgin Islands): 66 specimens.

Definition

The Cavoliniinae have a fairly globular teloconch with an ellipsoidal cross-section; *Cavolinia inflexa* is narrower near the lateral spines and longer posteriorly. The peristome has a round curved dorsal lip (which is straight and pointed in *Cavolinia inflexa* and has a beak-like gutter stucture in *Diacavolinia*). There are latero-longitudinal slits with a conspicuous closing mechanism (two mecanisms in the case of *Diacavolinia*). The comma-shaped protoconch is in line with the teloconch having no clear-cut demarcation; in *Diacavolinia* there is a discarded protoconch and the apex ends in an irregular slit (there is no septum) (Spoel et al., 1993).
According to Jennings et al. (2010) the COI data show the existence of no subtantial regional variations among

the Atlantic locations of *C. uncinata* but sequence differences were detected between some regions "(Atlantic vs. SE Indian)"

The Cavoliniinae differ in terms of the dorsal ornamentation. The Atlantic specimens (except for *C. uncinata*) generally have a larger number of dorsal ribs than the Indo-pacific specimens:

– The-*inflexa* group: three dorsal ribs (Atlantic Ocean) or a single rib (Indo-Pacific area).

– The *gibbosa* group: seven ribs (in the Atlantic Ocean and Mediterranean Sea); five ribs (in the Indo-Pacific area); the specimens collected between the South Eastern Atlantic and to the South Western Indian area had an intermediate number of ribs between five and seven.

– The *uncinata* group: three ribs (in the Eastern tropical Atlantic Ocean and South-Tyrrhenian sediments); five ribs (in the Western North Indian Ocean and Western Equatorial Pacific Ocean (Rampal, 1979).

The parapodia are very elongated and the posterior footlobe is short but very broad. The anterior appendages of the mantle are similar to those observed in the other Cavoliniidae; *Diacavolinia* species and *Cavolinia globulosa* also have two antero-ventral three-lobed expansions and are sometimes deciduous (**Fig. 3. C, E**). There are long and retractile lateral appendages (**Fig. 4**). The pallial gland is similar to those observed in the other Cavoliniidae (**Fig. 5. H**). The median teeth of the radula have a triangular base with long denticles and a curved triangular cuspid (**Figs 9, 10**).

The *Diacavolinia* species have a separate genital aperture (Meisenheimer, 1905).

Cladistic and molecular analyses (Figs 16-19)

Cladistic & 28S tree given congruent results: Cavoliniinae formed a monophyletic group.

– Cladistic: *Cavolinia* and *Diacavolinia* belong to the Cavoliniinae Gray, 1850.

– 28S mol. data and gene data set: the Cavoliniinae are monophyletic; *Cavolinia* is paraphyletic because of *C. globulosa*: (1.00/98, 1.00/90): *Diacavolinia* (Caribbean Sea) is the sister-group to *C. globulosa* (North Indian Ocean); nevertheless this group forms a monophyletic clade with the other Cavoliniinae.

– 28S: when noisy site were removed: *Diacavolinia* (Caribbean Sea) is the sister-group to *Cavolinia labiata* (Cap Town) & *Cavolinia* sp. (South-Western Indian Ocean).

– COI data and data set: the Cavoliniinae are polyphyletic because *Cavolinia inflexa* is basal to a clade composed of the other straight shell Euthecosomata (not including *Hyalocylis* and *Limacina helicina*).

The position of this Cavolininae species did not make sens.

– COI data: *Diacavolinia* (Mozambic Channel) is nested within *Cavolinia labiata* and *Cavolinia* sp. (South-Western Indian Ocean.

Conclusion

The status of *Diacavolinia* was validated using DNA Barcoding methods (Mass et al., 2013). This genus has some distinct characteristics (a deciduous protoconch, two closing mechanisms, and distinct genital orifices). However our molecular analyses (Corse et al., 2013) also showed the existence of some affinities between *Diacavolinia* and *Cavolinia labiata, C. globulosa* and *Cavolinia sp.*: the idea that the *Diacavolinia* genus was nested within these *Cavolinia* seems to be no longer valid. However it is difficult to explain the topological differences observed in this subfamily (monophyly or polyphyly), as well as the aberrant unlikely attribution of some species to the same group (cf. *Cavolinia inflexa* and *C. labiata*) and the position of *Cavolinia inflexa* as the sister group to all the straight shaped Euthecosomata (except for *Hyalocylis*). Further analyses are now required to elucidate these issues. The genus *Diacavolinia* is therefore temporary maintained.

Distribution

In the circum-global TARA Oceans samples: the Cavoliniinae accounted for 18% of the Cavoliniidae

Genus *Cavolinia* Abildgaard, 1791

– *Gibbosa* group: *Cavolinia gibbosa* (d'Orbigny, 1834): South-Western Indian Ocean, Mozambic Channel and Benguela Current (South-Eastern Atlantic Ocean). *Cavolinia flava* (d'Orbigny, 1834): all over the Atlantic Ocean and in two other rare situations: an exceptional incursion into the Western Mediterranean Sea near Gibraltar (where it is an Atlantic indicator current) and a few specimens observed in the North-Eastern Pacific near Panama (where it is a pre-isthmatic Atlantic palaeo-indicator); the latter area constitutes a faunistic entity in the Pacific Ocean (Rampal 2002; 2014). *Cavolinia plana* (Meisenheimer, 1905) is a characteristic Indo-Pacific species. It has been found to occur in the Indo-Austral Archipelago (Tesch 1904), throughout the Indo-Western Pacific (Rampal, 1975) and only rarely in the South-Eastern Pacific (Meisenheimer, 1905). *C. gibboides* Rampal, 2002 is only present in the Eastern Mediterranean Sea-South-Tyrrhenian Sea, where it is an endemic species (Rampal, 1970b, 1975). Unfortunally the very old specimens (mission Thor, 1910) did not yield any molecular relevant information about *C. gibboides* (Corse et al., 2013).

– *Inflexa* group: *Cavolinia inflexa imitans* (Pfeffer, 1880) has a cicumglobal distribution. *Cavolinia inflexa inflexa* (Lesueur, 1813) inhibits the border of the *C. i. imitans* range of distribution. *Cavolinia labiata* (d'Orbigny, 1834) inhabits the Indo-Pacific region, especially the Mozambic Channel with an incursion in the South Eastern Atlantic Ocean. The sporadic presence of *Cavolinia inflexa* in the North-Eastern Pacific Ocean suggests that it may be a pre-isthmatic palaeo-indicator (Rampal, 2002).

Cavolinia labiata and *C. inflexa* (1.00/99) have be found at the same station without showing any hybridization.

– *Tridentata* group: despite the existence of considerable polymorphism, two morphological tendencies have been observed. One of which involved *tridentata* (which has a broad worldwide pattern of distribution) and the other one, *affinis* (d'Orbigny, 1836) (which is almost practically restricted to the Eastern Pacific Ocean). However a projection of correspondence analyses has shown the existence of a series of affinities between the populations inhabiting various oceans. This results in a circum-global cline with a belt of hybrid populations in the South-Eastern Pacific Ocean (Rampal, 1975). Although each area has a characteristic phenotype, the morphotype usually shows affinities with those in neighbouring areas with which they form a clinal variations.

– *Uncinata* group: this tropical group is present in all the ocean of the World (with the possible exception of the Mediterranean Sea?). There exist both Indo-Pacific and Atlantic entities. Spoel (1969) described three taxa: *Cavolinia uncinata* f. *uncinata* (Rang, 1828) (L =6.97 mm), and *C. u. roperi* Spoel, 1969 (L =4.48 mm) the Atlantic Ocean, and *C.u. pulsata* Spoel, 1969 (L =8.14 mm) in the Indian Ocean. The Indian specimens collected were the largest ones (Rampal, 1979).
According to Jennings et al. (2010) the COI data shows the presence of no substantial regional variations in *C. uncinata* between the Atlantic locations but the sequence differences were detected between different area "(Atlantic v.s. SE Indian)".

– *Cavolinia globulosa* (Gray, 1850): Indo-Pacific species.

Genus *Diacavolinia* Spoel, 1987

The polymorphic and polytypic recent *Diacavolinia* genus is present in all the Oceans of the World (although it is fairly rare in the Mediterranean Sea). According to Spoel et al. (1993) the following locations are the most characteristic of the genus.
In the Atlantic Ocean: *D. atlantica, D. deblainvillei, D. ovalis, D. deshayesi, D. constricta, D. strangulata, D. longirostris, D. limbata.*
In the Indian Ocean: *D. bicornis, D. souleyeti, D. striata, D. aspina*. Red Sea: *D. flexipes.*
Pacific Ocean: *D. pacifica, D. vanutrechti, D. triangulata, D. robusta, D. mcgowani,*
Around Malaisia: *D. vanutrechti, D. elegans, D. bandaensis.*
In the Atlantic, Indian and Pacific Ocean: *D. angulosa.*

New classification

Order Thecosomata de Blainville, 1824
Suborder Euthecosomata Meisenheimer, 1905

Family Limacinidae Gray, 1847
Genus *Limacina* Bosc, 1817; *Limacina helicina* (Phipps, 1774)
Family **Heliconoididae** Rampal, 2017
Genus *Heliconoides* d'Orbigny, 1835; *Heliconoides inflata* (d'Orbigny, 1835)
Family **Thieleidae** Rampal, 2017
Genus *Thielea* Strebel, 1908; *Thielea helicoides* (Jeffreys, 1877)

Superfamily Cavolinioidea Gray, 1850
Family Creseidae Rampal, 1973
Genus *Creseis* Rang, 1828; *Creseis virgula* (Rang, 1828)
Genus ***Boasia*** Dall, 1889; *Boasia chierchiae* (Boas, 1886) Rampal, 2017.
Family Cavoliniidae Gray, 1850
Subfamily Cuvierininae Spoel, 1967
Genus *Cuvierina* Boas, 1886; *Cuvierina columnella* (Rang, 1827)
Subfamily Cliinae Jeffreys, 1869
Genus *Clio* Linnaeus, 1767; *Clio pyramidata* Linnaeus, 1767
Genus ***Hyalaea*** de Blainville, 1821; *Hyalaea cuspidata* Boas, 1802
Subfamily **Diacriinae** Rampal, 2017
Genus *Diacria* Gray, 1847; *Diacria trispinosa* (de Blainville, 1821)
Genus ***Telodiacria*** Rampal, 2017; *Telodiacria quadridentata* (de Blainville, 1821) Rampal, 2017
Subfamily Cavoliniinae Gray, 1850
Genus *Cavolinia* Abildgaard, 1791; *Cavolinia tridentata* (Niebuhr, 1775)
Genus *Diacavolinia* Spoel, 1987; *Diacavolinia longirostris* (Spoel, 1987)

Genera *Incertae sedis*
Genus *Styliola* Gray, 1850; *Styliola subula* (Quoy & Gaimard, 1827)
Genus *Hyalocylis* Fol, 1875; *Hyalocylis striata* (Rang, 1828)

Phylogenetic hypotheses

The Thecosomata are thought to be considered neotenic organisms originating from spiral benthic ancestors (Lemche, 1948; Huber, 1993). This hypothesis has not been fully accepted especially by Lalli and Gilmer (1989). The spiral shell corresponds to the plesiomorphic state of the Euthecosomata. The characteristic left-handed spiral shell has been allocated to the neotenic extension of larval features observed in benthic forms. The postmetamorphic ontogenic 'retainement of the sinistral coiling of the shell as well as reshaping of the juvenile shell in *Diacria* spp. and *Cavolinia* spp. are unique features of the euthecosomatous pteropods' (Bandel et al., 1984; Bandel & Hemleben, 1995).
The emergence of the holoplanktonic Euthecosomata from benthic Gastropoda resulted from successive radiations from the Upper Paleocene until the Pliocene. These events involved considerable morphological and anatomical changes: the acquisition of swimming organs in the spiral shell Euthecosomata, followed by the transition to a straight shell, which was subsequently gradually optimised. According to Haszprunar (1985) the

Euthecosomata's structure illustrates the paedomorphic aspect of the shell's long development. Some taxa either became extinct or their diversity decreased during the Tertiary era, but interestingly, *Limacina* Bosc, 1817, *Creseis* Rang, 1828 and *Cuvierina* Boas, 1886 are still present. The first spiral Euthecosomata, Heliconoididae and Limacinidae, appeared during the Late Paleocene (58.6 MY) - Early Eocene (56.5 MY) (Hodgkinson et al., 1992). The first perfect straight Euthecosomata, *Creseis*, appeared during the Middle Eocene. The transition from the spiral shells to straight ones is illustrated by the partially uncoiled species, also observed during the course of ontogenesis (Fol, 1875).

1. Based on morphological and anatomical data, two phylogenetic hypotheses were originally put forward.
– A single event was proposed in a case of all the Cavolinioidea Gray, 1850 from a single spiral shell lineage (Boas, 1886, Pelseneer, 1888, Meisenheimer, 1905, Bonnevie, 1913, Richter, 1973).
– Two events in that of the Creseidae Rampal, 1973 and Cavoliniidae Gray, 1850 from two spiral shell lineages: Limacinidae (*Limacina* + *Heliconoides*) and Thieleidae (*Thielea*) (Rampal, 1973).

2. Based on molecular analyses two pylogenetic hypotheses was proposed:
– COI phylogenetic tree (**Figs 16, 17**): the straight-shell species may possibly have emerged twice independently due to a reversal of the lineage *Thielea* / *Heliconoides* (Corse et al., 2013). In addition according to the latest palaeontological knowledge, *Clio* occurred during the Lower Oligocene and the radiation of *Cavolinia* occured during the Early Miocene, long after the first straight shell *Creseis* like fossils. However this chronology is not in agreement with the COI tree in which *Cavolinia* branched before the divergence occurred between the *Creseis* and *Cuvierina* lineages. This scenario involving a two-fold pattern of emergence was also not adopted in the end because it is less parsimonious in terms of the corresponding morphological changes and less informative about the previous divergence events (Corse et al., 2013).

Comment: a two-fold pattern of emergency was also observed in the COI tree by Jennings et al. (2010): *Heliconoides inflata* is the sister group to *Creseis* and *Thielea helicoides* is the sister group to the Euthecosomata (not including *Limacina helicina* and *Hyalocylis striata*). These authors did not reach any phylogenetical conclusion however, on account of 'their poor taxonomic sampling'.
– 28S phylogenetic tree (**Figs 18, 19**) suggested the occurrence of a single emergence. The straight-shell species of Cavolinioidea Gray, 1850 originated from a single coiled-shell ancestor which subsequently evolved into a straight conical morphotype belonging to the genus *Creseis* which then gave rise to the more complex straight shells of the Cavoliniidae Gray, 1850. This hypothesis is the most informative about the previous divergence event (Corse et al., 2013).
We have kept this hypothesis about the monophyly. The incongruence between gene trees may also have resulted from incomplete lineage sorting processes (absence of data resolution in 28S gene data set and in 28S molecular data for *Thielea*; absence in 28S gene data set for *Heliconoides*). It should be emphasised that these interpretations may have to be revised in the light of future studies on currently available 28S sequences of *Heliconoides inflata* and *Thielea helicoides*.

As far as the origin of the helicoidal calcareous microstructure of the straigt shell is concerned, the following hypothesis was proposed to explain the impact of the spiral shells macro-unwinding on their prismatic and crossed-lamellar fibres. Result: the straight shells have helicoidal microfibres (Rampal, 1972; 1973, 1975). The helicoidal microstructure is also present in the partly unwounding fossil *Camptoceratops priscum* (Gowin-Austen, 1925) (Curry & Rampal, 1979), which can also been observed near the apex of *Heliconoides inflata* (Glaçon et al., 1994, pl. 3, figs 1-9) and that of *Limacina retroversa* (**Fig. 6. F**). This helicoidal microscruture in the apex-protoconch of the spiral Euthecosomata might be the precursory anticiped plan of this macro-unwinding process. A similar helicoidal aragonitic microstructure has been observed in the meroplanktonic veligers of some benthic Tectibranch molluscs (Richter, 1976).
According to Poulicek et al. (1991) 'the mechanical characteristics of these very light shells allow flexibility and reduce their brittleness'

Discussion

Taxonomy

Spiral Euthecosomata: Limacinidae Gray, 1847; Heliconoididae Rampal, 2017; Thieleidae Rampal, 2017.
Straight Euthecosomata: Cavolinioidea Gray, 1850: Creseidae Rampal, 1973; Cavoliniidae Gray, 1850: Cuvierininae Spoel, 1967; Cliinae Jeffreys, 1869; Diacriinae Rampal, 2017; Cavoliniinae Gray, 1850.
Styliola Gray, 1850 and *Hyalocylis* Fol, 1875 are now taken to be *incertae sedis*.
The following genera are new or restored: *Telodiacria* n. gen. (Rampal, 2017), *Boasia* Dall, 1889, *Hyalaea* de Blainville, 1821. The precedence of *Creseis acicula* has been confirmed ICZN case 3758 (Rampal, 2017). *Cuvierina columnella* f. *atlantica* Spoel, 1970 is replaced by *C. major* nomen novum. The taxonomic rank of most of the species is new or confirmed. The fossil *Altaspiratella* Korobkov, 1966 has been excluded from the Limacinidae Gray, 1847 because of the absence of an umbilicus and the presence of a similar twisted columella to that observed in the Peraclididae Tesch, 1913. The Peraclididae emerged during the Early Eocene with *Altaspiratella*. They have been reappeard during the Oligocene with *Peracle*. Its integration in the Peraclididae lineage can be tested in the integrative approach to the estimation of the divergence time. In the meantime *Altaspiratella* is a genus *incertae sedis*. A similar pattern event occurd in

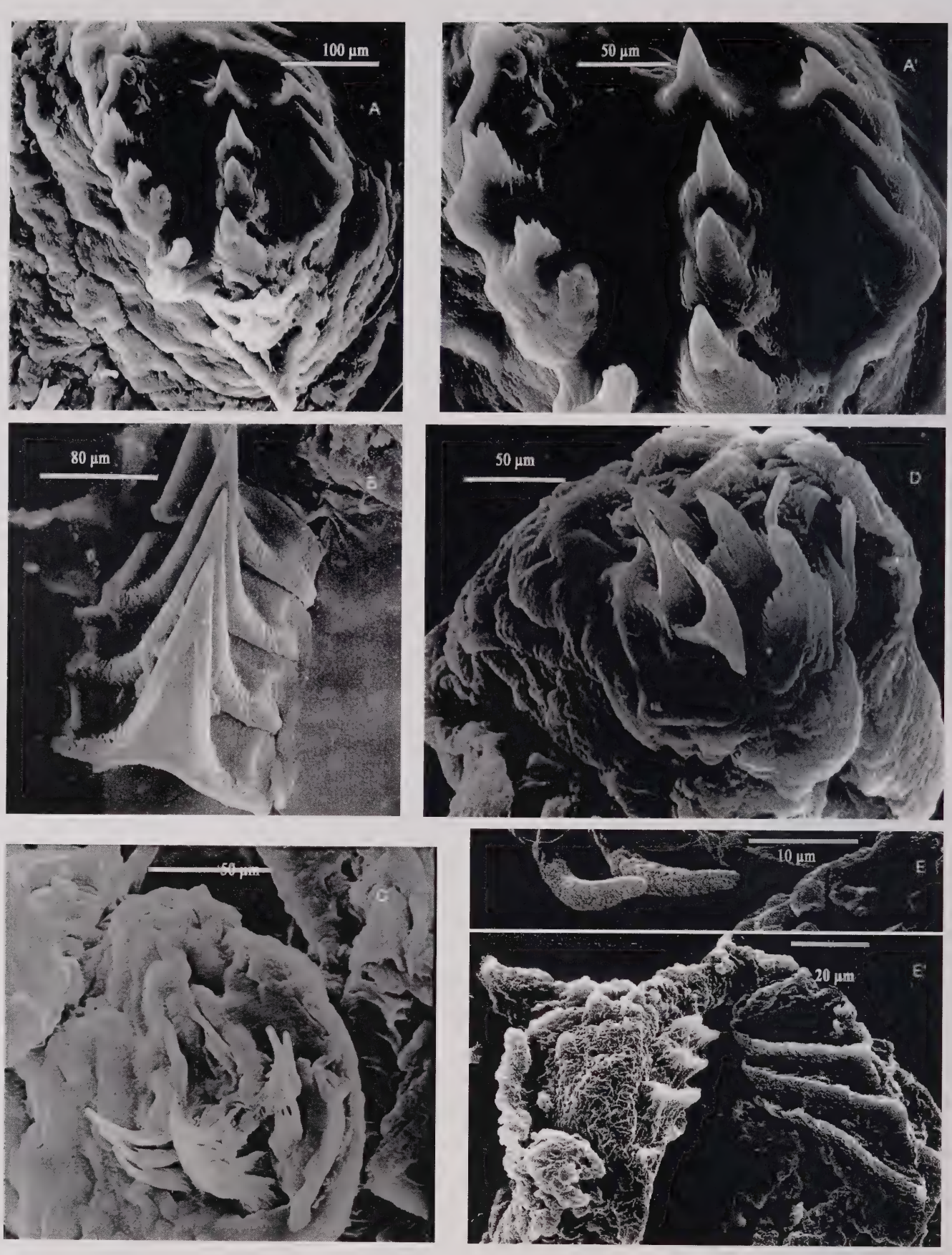


Fig. 7. Radula and jaw. (SEM microphotographs). **A-E**. radula: **A, A'**. *Thielea helicoides* (Jeffreys, 1877); **B**. *Cuvierina columnella* (Rang, 1827); **C**. *Styliola subula* (Quoy & Gaimard, 1827); **D**. *Hyalocylis striata* (Rang, 1828). **E'**. *Hyalocylis* (singular specimen); **E'**. jaw.

Fig. 7. Radula e mandibola (microfotografie al SEM). **A-E**. radula: **A, A'**. *Thielea helicoides* (Jeffreys, 1877); **B**. *Cuvierina columnella* (Rang, 1827); **C**. *Styliola subula* (Quoy & Gaimard, 1827); **D**. *Hyalocylis striata* (Rang, 1828). **E'**. *Hyalocylis* (singolo esemplare); **E'**. mandibola.

the *Hyalocylis* lineage which started earlier (Lower Oligocene) with *Prehyalocylis* and reappeared wiith *Hyalocylis* (Upper Miocene).

The integrative approach to the estimation of divergence times is also powerful tool which could be used to elucidate the late emergence of the phenotypical

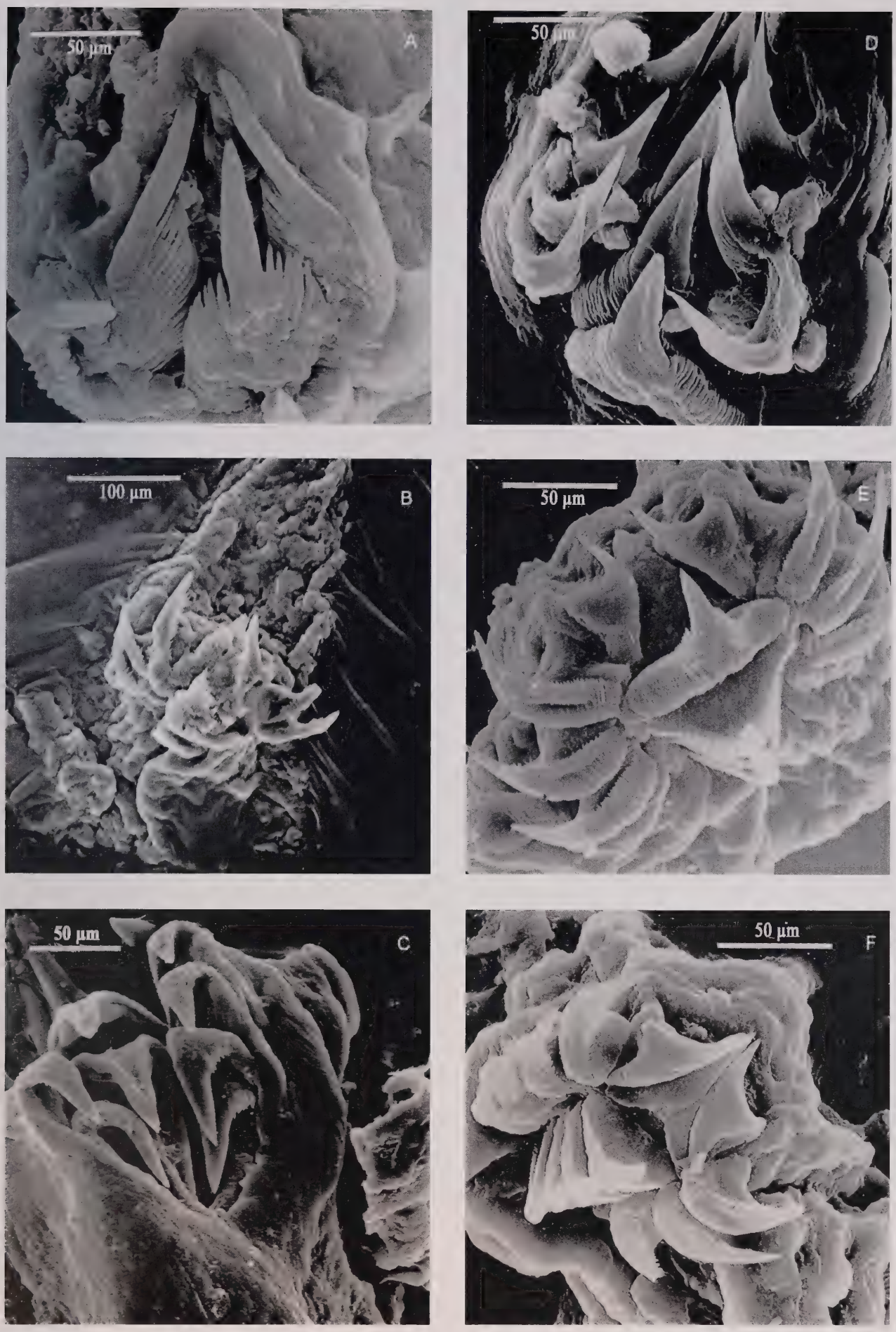


Fig. 8. Radula (SEM microphotographs). **A**. *Clio pyramidata* Linnaeus, 1767; **B**. *Clio convexa* (Boas, 1886); **C**. *Clio recurva* (Childern, 1823); **D**. *Hyalaea cuspidata* (Bosc, 1802); **E**. *Diacria trispinosa* (de Blainville, 1821); **F**. *Diacria rampalae* Dupont, 1979.

Fig. 8. Radula (microfotografie al SEM). **A**. *Clio pyramidata* Linnaeus, 1767; **B**. *Clio convexa* (Boas, 1886); **C**. *Clio recurva* (Childern, 1823); **D**. *Hyalaea cuspidata* (Bosc, 1802); **E**. *Diacria trispinosa* (de Blainville, 1821); **F**. *Diacria rampalae* Dupont, 1979.

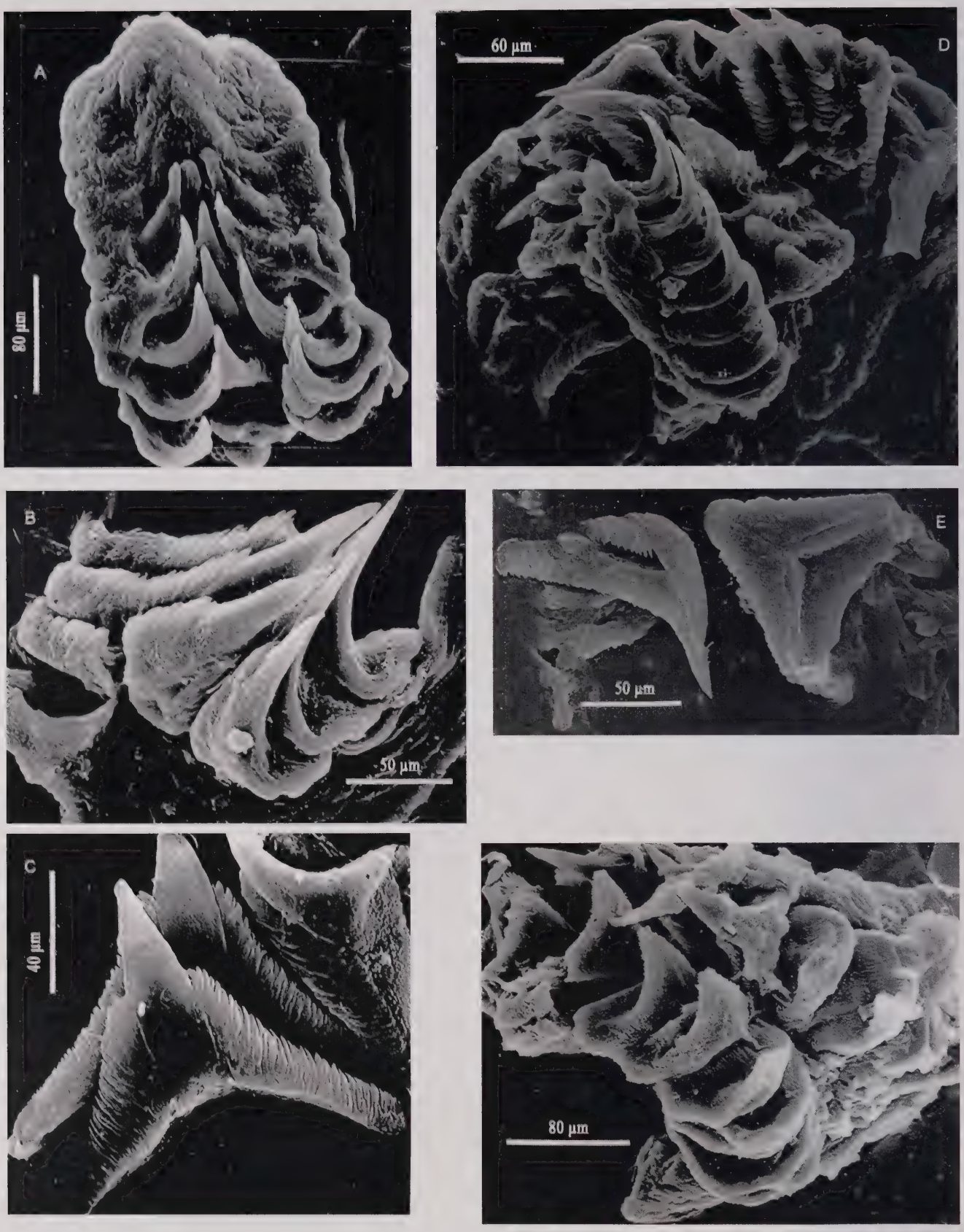


Fig. 9. Radula (SEM microphotographs). **A, B**. *Cavolinia globulosa* (Gray, 1850) (**A**. Indian Ocean; **B**. Pacific Ocean); C, *Cavolinia* sp.; **D, E**. *Cavolinia inflexa imitans* (Lesueur, 1813); **F**. *Cavolinia tridentata* (Niebuhr, 1775).

Fig. 9. Radula (microfotografie al SEM). **A, B**. *Cavolinia globulosa* (Gray, 1850) (**A**. Oceano Indiano; **B**. Oceano Pacifico); C, *Cavolinia* sp.; **D, E**. *Cavolinia inflexa imitans* (Lesueur, 1813); **F**. *Cavolinia tridentata* (Niebuhr, 1775).

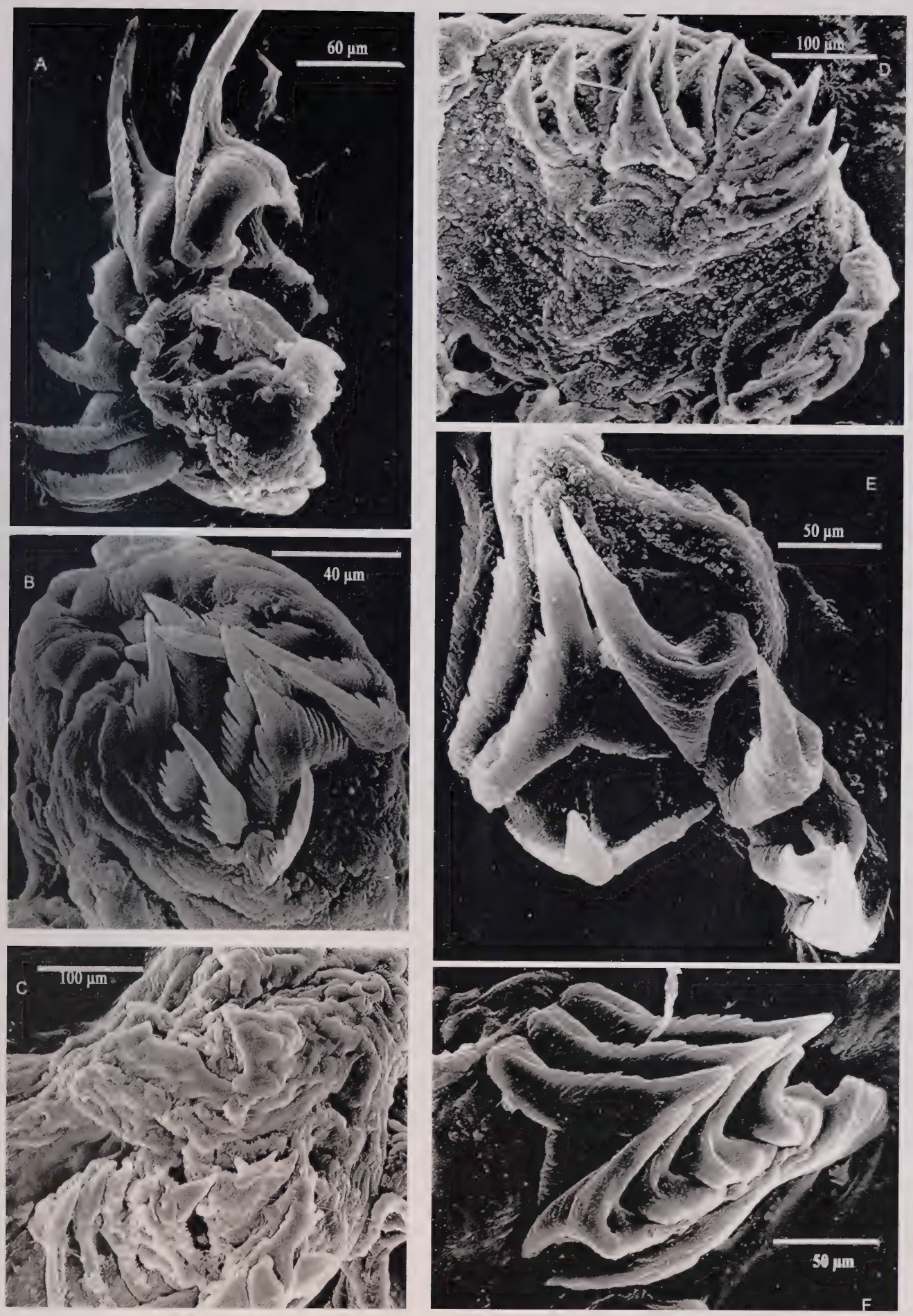
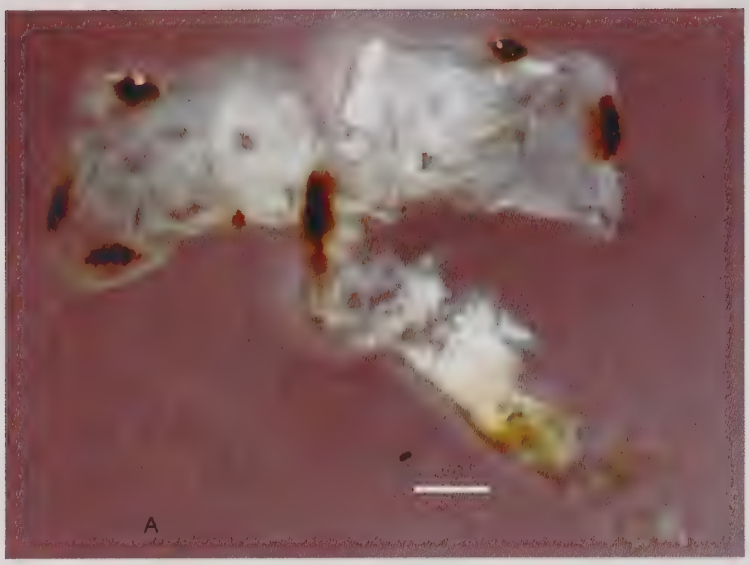


Fig. 10. Radula (SEM microphotographs). **A**. *Cavolinia plana* Meisenheimer, 1905; **B**. *Cavolinia gibboides* Rampal, 2002; **C**. *Cavolinia flava* (d'Orbigny, 1834); **D, E, F**. *Diacavolinia* sp. Spoel, 1987.

Fig. 10. Radula (microfotografie al SEM). **A**. *Cavolinia plana* Meisenheimer, 1905; **B**. *Cavolinia gibboides* Rampal, 2002; **C**. *Cavolinia flava* (d'Orbigny, 1834); **D, E, F**. *Diacavolinia* sp. Spoel, 1987.



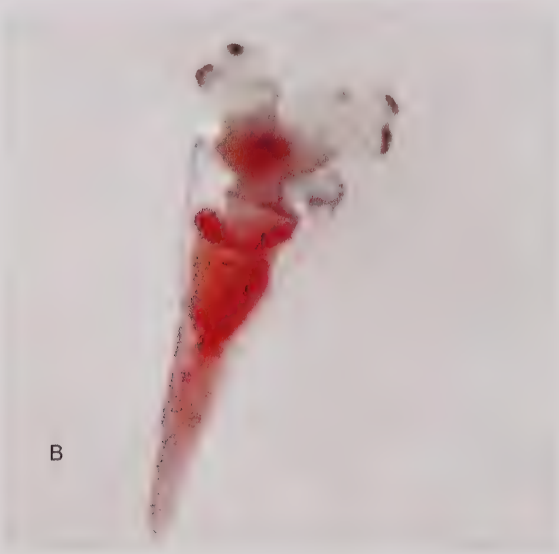


Fig. 11. *Hyalocylis striata* (Rang, 1828) (new species?): **A**. breack adulte without shell; **B**. young specimen (photographs, G. Neve).

Fig. 11. *Hyalocylis striata* (Rang, 1828) (nuova specie?): **A**. adulto rotto senza conchiglia; **B**. giovane esemplare (fotografie, G. Neve).

complexe *Thielea helicoides* (Jeffreys, 1877) and of the plesiomorphic *Clio polita* (Pelseneer, 1888).
The fossil *Vaginella* Daudin, 1800 has been integrated into the Cuvierininae.
The process of neoteny seems to look place in the case of the genus *Styliola*.

Phylogeny

Two phylogenetic hypotheses were originally put forward.
The first one was based on the two-fold emergency of straight shell species from two separate lineages of spiral shell ancestors (Rampal, 1973). According to the COI phylogenetic tree the emergence of these species did indeed involve two events (Corse et al., 2013).
However the 28S tree did not support this scenario wich is the less parsimonious of the two. We have adopted the second hypothesis which is based on the monophyly of Euthecosomata (Corse et al., 2013). The congruence of this hypothesis with our cladistic and molecular (28S) supports this interpretation. We have concluded that the first transition from a spiral shell morphotype into the first plesiomorphic straight conica shell (*Creseis*) may have subsequently given rise to all the other genera with apomorphic straight shells. These conclusions therefore required some reserves and further investigations (Corse et al., 2013).

Acknowledgements

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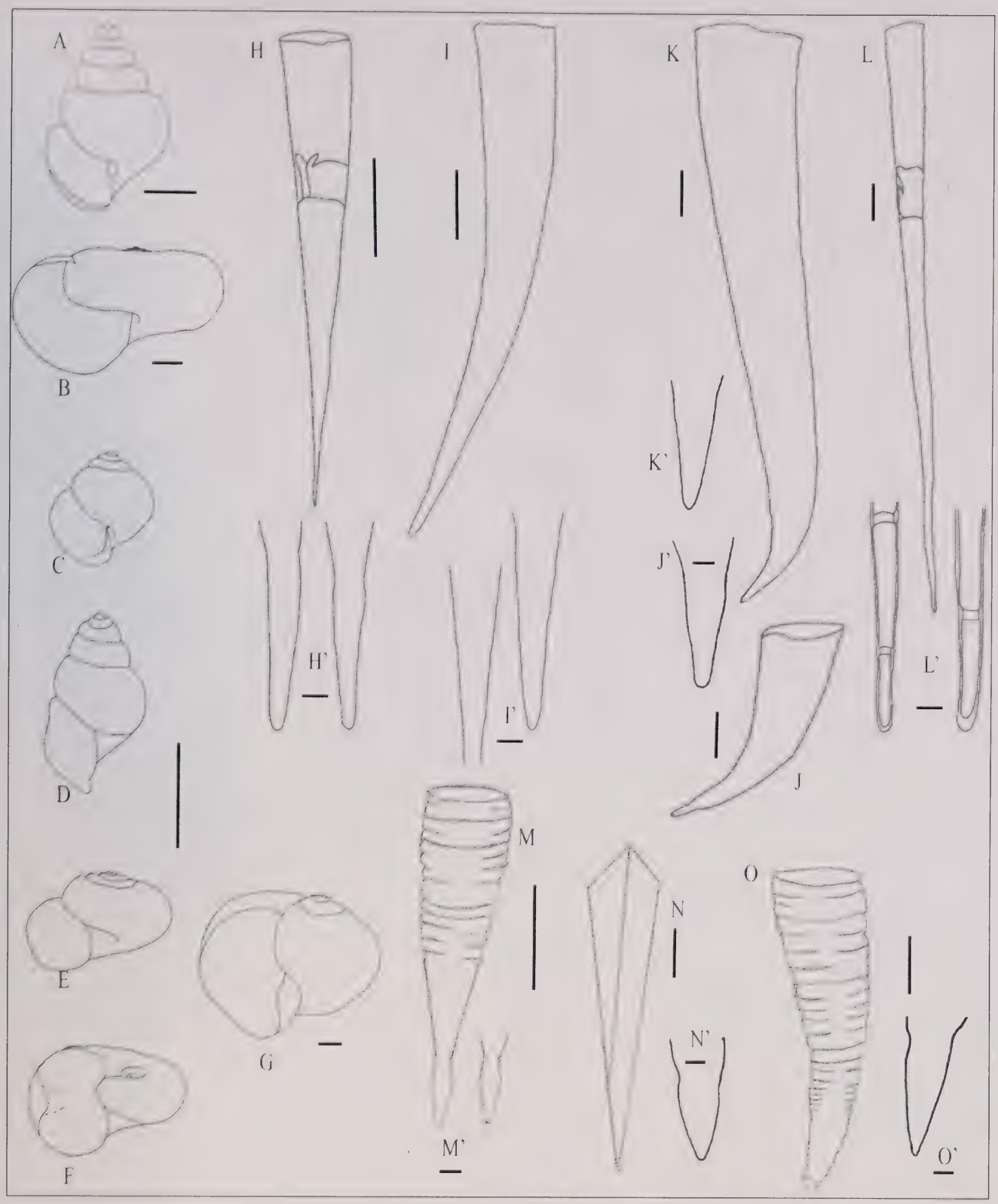

Fig. 12. Euthecosomata Meisenheimer, 1905: teloconch and protoconch (oral or lateral views). **A**. *Limacina retroversa* (Flemming, 1823); **B**. *Limacina helicina* (Phipps, 1774); **C**. *Limacina trochiformis* (d'Orbigny, 1836); **D**. *Limacina bulimoides* (d'Orbigny, 1836); **E**. *Limacina lesueurii* (d'Orbigny, 1836); **F**. *Heliconoides inflata* (d'Orbigny, 1835); **G**. *Thielea helicoides* (Jeffreys, 1877); **H, H'**. *Creseis conica conica* Escholtz, 1829; **I, I'**, *Creseis conica falsiparum* Rampal, 2002; **J, J'**. *Creseis virgula virgula* (Rang, 1828); **K, K'**. *Creseis virgula frontieri* Rampal, 2002; **L, L'**. *Creseis acicula* (Rang, 1828); **M, M'**. *Boasia chierchiae* (Boas, 1886) Rampall, 2017; **N, N'**. *Styliola subula* (Quoy & Gaimard, 1827); **O, O'**. *Hyalocylis striata* (Rang, 1828). Scale: 1 mm.

Fig. 12. Euthecosomata Meisenheimer, 1905: teleoconca e protoconca (vista orale o laterale). **A**. *Limacina retroversa* (Flemming, 1823); **B**. *Limacina helicina* (Phipps, 1774); **C**. *Limacina trochiformis* (d'Orbigny, 1836); **D**. *Limacina bulimoides* (d'Orbigny, 1836); **E**. *Limacina lesueurii* (d'Orbigny, 1836); **F**. *Heliconoides inflata* (d'Orbigny, 1835); **G**. *Thielea helicoides* (Jeffreys, 1877); **H, H'**. *Creseis conica conica* Escholtz, 1829; **I, I'**, *Creseis conica falsiparum* Rampal, 2002; **J, J'**. *Creseis virgula virgula* (Rang, 1828); **K, K'**. *Creseis virgula frontieri* Rampal, 2002; **L, L'**. *Creseis acicula* (Rang, 1828); **M, M'**. *Boasia chierchiae* (Boas, 1886) Rampall, 2017; **N, N'**. *Styliola subula* (Quoy & Gaimard, 1827); **O, O'**. *Hyalocylis striata* (Rang, 1828). Scala: 1 mm.

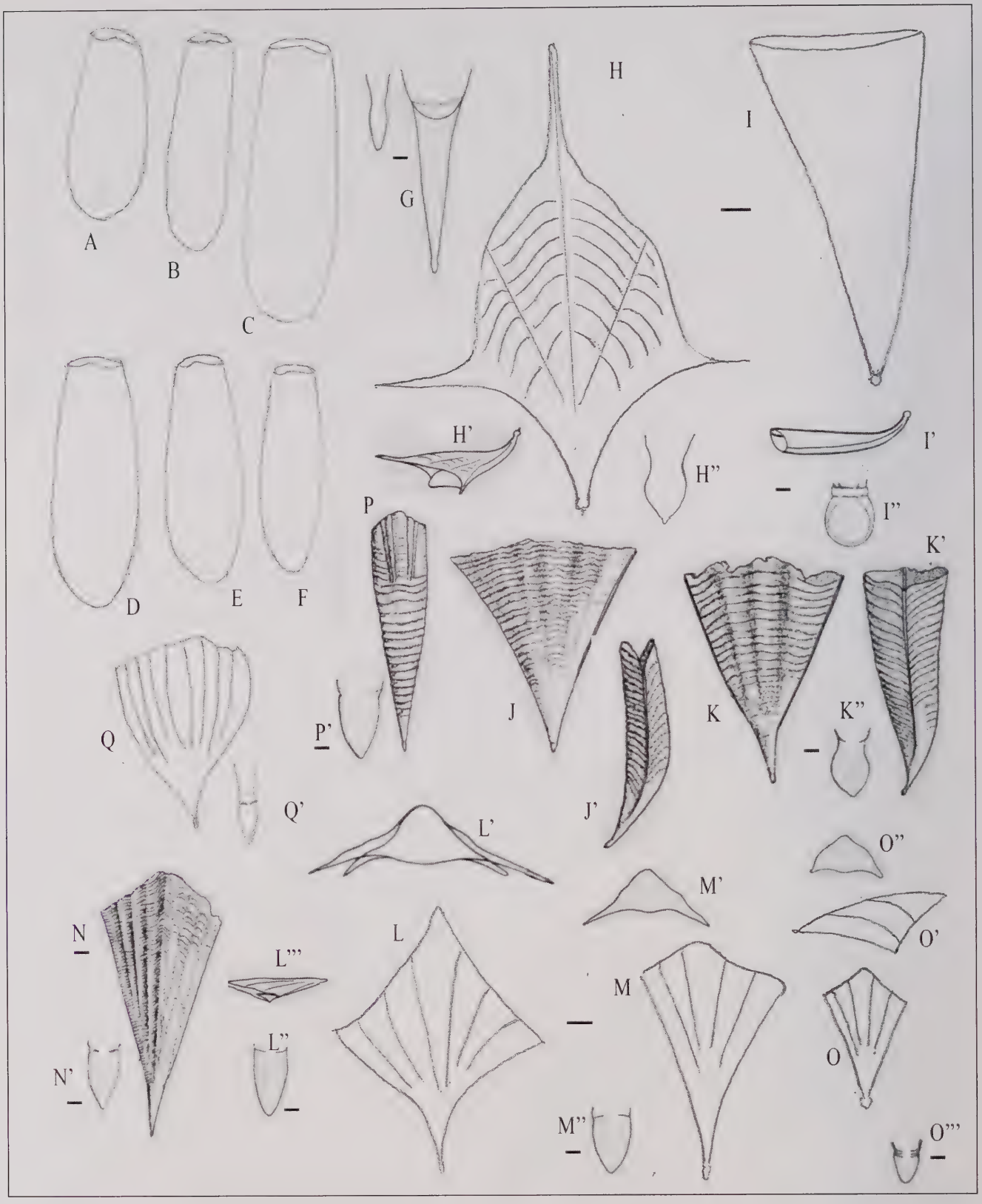

Fig. 13. Euthecosomata Meisenheimer, 1905: teloconch (ventral, dorsal, lateral or oral views), protoconch. **A**. *Cuvierina urceolaris* (Mörch, 1850); **B**. *Cuvierina columnella* (Rang, 1827); **C**. *Cuvierina major* Rampal, *nomen novum*; **D**. *Cuvierina cancapae* Janssen, 2005; **E**. *Cuvierina pacifica* Janssen, 2005; **F**. *Cuvierina tsudai* Burridge et al., 2016; **G**. younger shell and conical protoconch; **H-H"**. *Hyalaea cuspidata* (Bosc, 1802); **I-I"**. *Clio polita* (Pelseneer, 1888); **J, J'**. *Clio chaptali* Gray, 1850; **K-K"**. *Clio recurva* (Childern, 1823); **L-L'"**. *Clio pyramidata lanceolata* (Lesueur, 1813); **M-M"**. *Clio pyramidata pyramidata* Linné, 1767; **N, N'**. *Clio pyramidata sulcata* (Pfeffer, 1879); **O-O'"**. *Clio convexa* (Boas, 1886); **P, P'**. *Clio antarctica* Dall, 1908; **Q, Q'**. *Clio excisa* Spoel, 1963. Scale: 1 mm (teloconch), 0.1 mm (protoconch).

Fig. 13. Euthecosomata Meisenheimer, 1905: teleoconca (vista ventrale, dorsale, laterale o orale), protoconca. **A**. *Cuvierina urceolaris* (Mörch, 1850); **B**. *Cuvierina columnella* (Rang, 1827); **C**. *Cuvierina major* Rampal, *nomen novum*; **D**. *Cuvierina cancapae* Janssen, 2005; **E**. *Cuvierina pacifica* Janssen, 2005; **F**. *Cuvierina tsudai* Burridge et al., 2016; **G**. conchiglia più giovane e protoconca conica; **H-H"**. *Hyalaea cuspidata* (Bosc, 1802); **I-I"**. *Clio polita* (Pelseneer, 1888); **J, J'**. *Clio chaptali* Gray, 1850; **K-K"**. *Clio recurva* (Childern, 1823); **L-L'"**. *Clio pyramidata lanceolata* (Lesueur, 1813); **M-M"**. *Clio pyramidata pyramidata* Linné, 1767; **N, N'**. *Clio pyramidata sulcata* (Pfeffer, 1879); **O-O'"**. *Clio convexa* (Boas, 1886); **P, P'**. *Clio antarctica* Dall, 1908; **Q, Q'**. *Clio excisa* Spoel, 1963. Scala: 1 mm (teleoconca), 0,1 mm (protoconca).

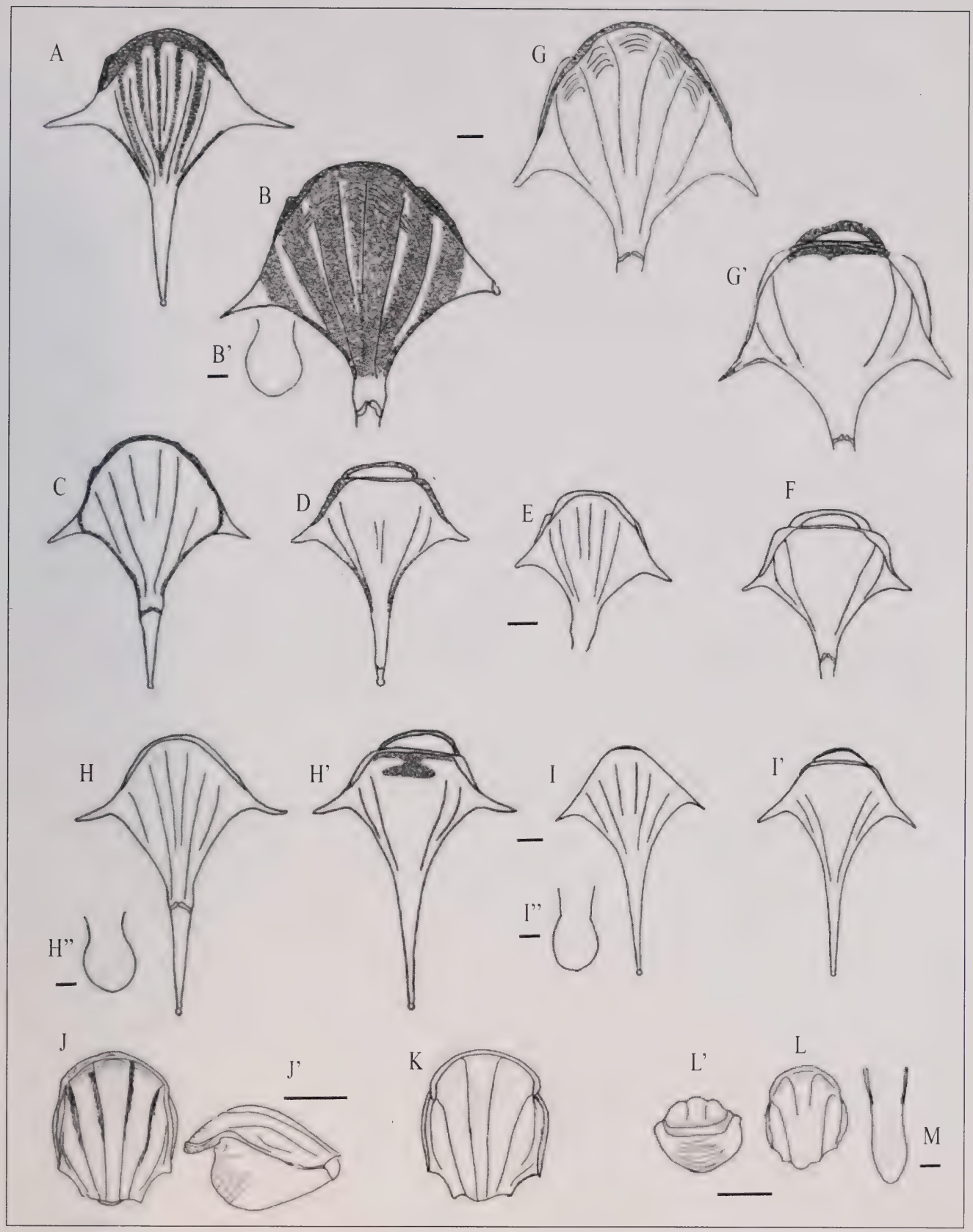

Fig. 14. Euthecosomata Meisenheimer, 1905: teloconca (dorsal, ventral, lateral or oral views), protoconch. **A-F**. *Diacria trispinosa* (de Blainville, 1821) (**A, B**. North Eastern Atlantic; **C, D**. South Eastern Atlantic; **E**. Central Pacific; **F**. Indian Ocean). **G, G'**. *Diacria major* (Boas, 1886); **H-H"**. *Diacria rampalae* Dupont, 1979; **I-I"**. *Diacria gracilis* Rampal, 2002; **J, J'**. *Telodiacria costata* (Pfeffer, 1879) Rampall, 2017; **K**. *Telodiacria quadridentata* (de Blainville, 1821) Rampall, 2017; **L, L'**. *Telodiacria danae* (Spoel, 1968) Rampall, 2017; **M**. *Telodiacria* Rampal, 2017, protoconch. Scale: 1 mm (teloconch), 0.1 mm (protoconch).

Fig. 14. Euthecosomata Meisenheimer, 1905: teleoconca (vista ventrale, dorsale, laterale o orale), protoconca. **A-F**. *Diacria trispinosa* (de Blainville, 1821) (**A, B**. Nord Est Atlantico; **C, D**. Sud Est Atlantico; **E**. Pacifico Centrale; **F**. Oceano Indiano). **G, G'**. *Diacria major* (Boas, 1886); **H-H"**. *Diacria rampalae* Dupont, 1979; **I-I"**. *Diacria gracilis* Rampal, 2002; **J, J'**. *Telodiacria costata* (Pfeffer, 1879) Rampall, 2017; **K**. *Telodiacria quadridentata* (de Blainville, 1821) Rampall, 2017; **L, L'**. *Telodiacria danae* (Spoel, 1968) Rampall, 2017; **M**. *Telodiacria* Rampal, 2017, protoconca. Scala: 1 mm (teleoconca), 0,1 mm (protoconca).

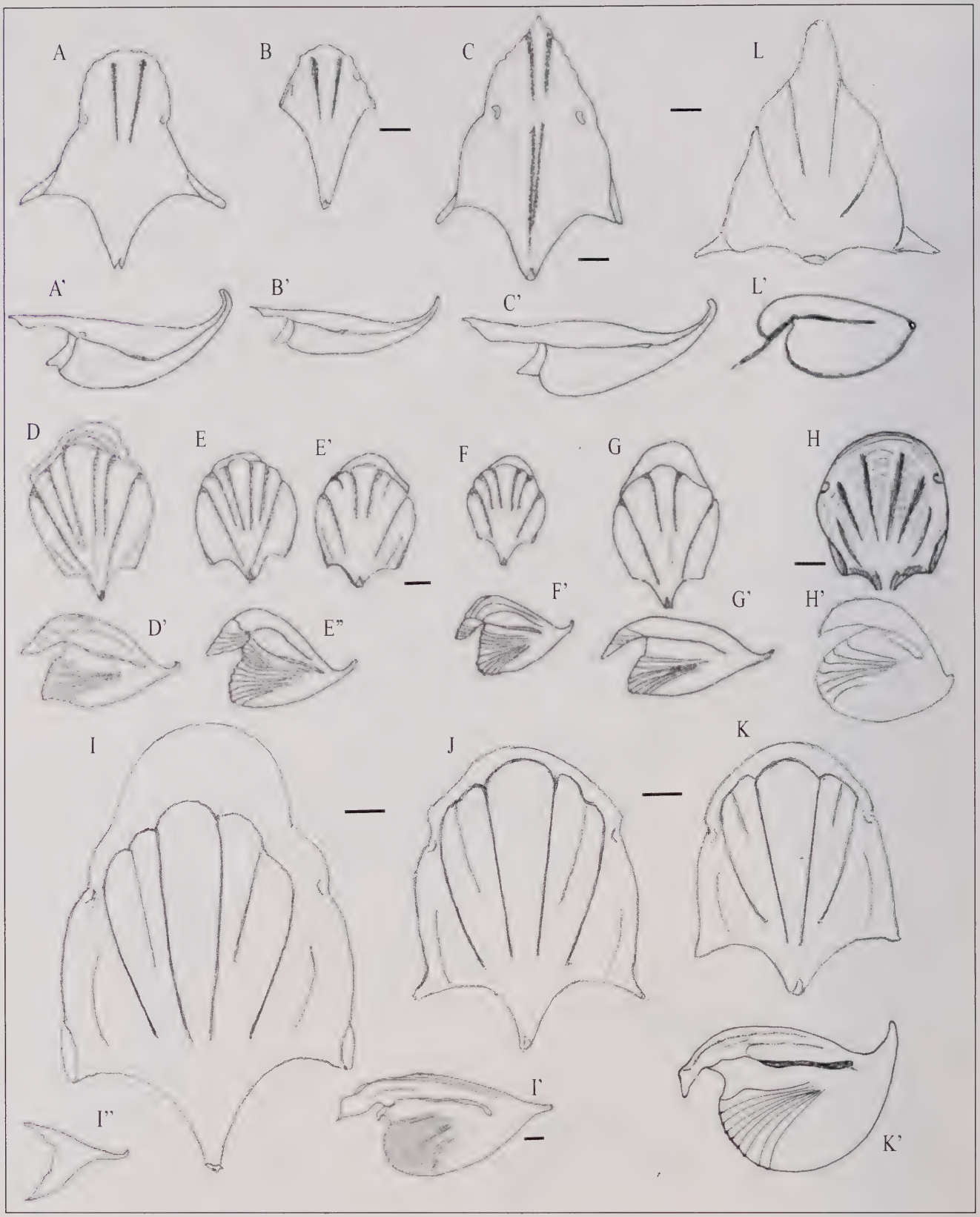

Fig. 15. Euthecosomata Meisenheimer, 1905: teloconch (dorsal or lateral views). **A, A'**. *Cavolinia inflexa imitans* (Pfeffer, 1880); **B, B'**. *Cavolinia inflexa inflexa* (Lesueur, 1813); **C, C'**. *Cavolinia labiata* (d'Orbigny, 1836); **D, D'**. *Cavolinia flava* (d'Orbigny, 1834); **E-E"**. *Cavolinia gibbosa* (d'Orbigny, 1834); **F, F'**. *Cavolinia gibboides* Rampal, 2002; **G, G'**. *Cavolinia plana* (Meisenheimer, 1905); **H, H'**. *Cavolinia globulosa* (Gray, 1850); **I-I"**. *Cavolinia tridentata* (Forskal, 1775); **J**. *Cavolinia uncinata pulsata* Spoel, 1969; **K, K'**. *Cavolinia uncinata uncinata* (Rang, 1829). **L, L'**. *Diacavolinia longirostris* Spoel, 1987; Scale: 1 mm.

Fig. 15. Euthecosomata Meisenheimer, 1905: teleoconch (vista dorsale o laterale). **A, A'**. *Cavolinia inflexa imitans* (Pfeffer, 1880); **B, B'**. *Cavolinia inflexa inflexa* (Lesueur, 1813); **C, C'**. *Cavolinia labiata* (d'Orbigny, 1836); **D, D'**. *Cavolinia flava* (d'Orbigny, 1834); **E-E"**. *Cavolinia gibbosa* (d'Orbigny, 1834); **F, F'**. *Cavolinia gibboides* Rampal, 2002; **G, G'**. *Cavolinia plana* (Meisenheimer, 1905); **H, H'**. *Cavolinia globulosa* (Gray, 1850); **I-I"**. *Cavolinia tridentata* (Forskal, 1775); **J**. *Cavolinia uncinata pulsata* Spoel, 1969; **K, K'**. *Cavolinia uncinata uncinata* (Rang, 1829). **L, L'**. *Diacavolinia longirostris* Spoel, 1987; Scala: 1 mm.

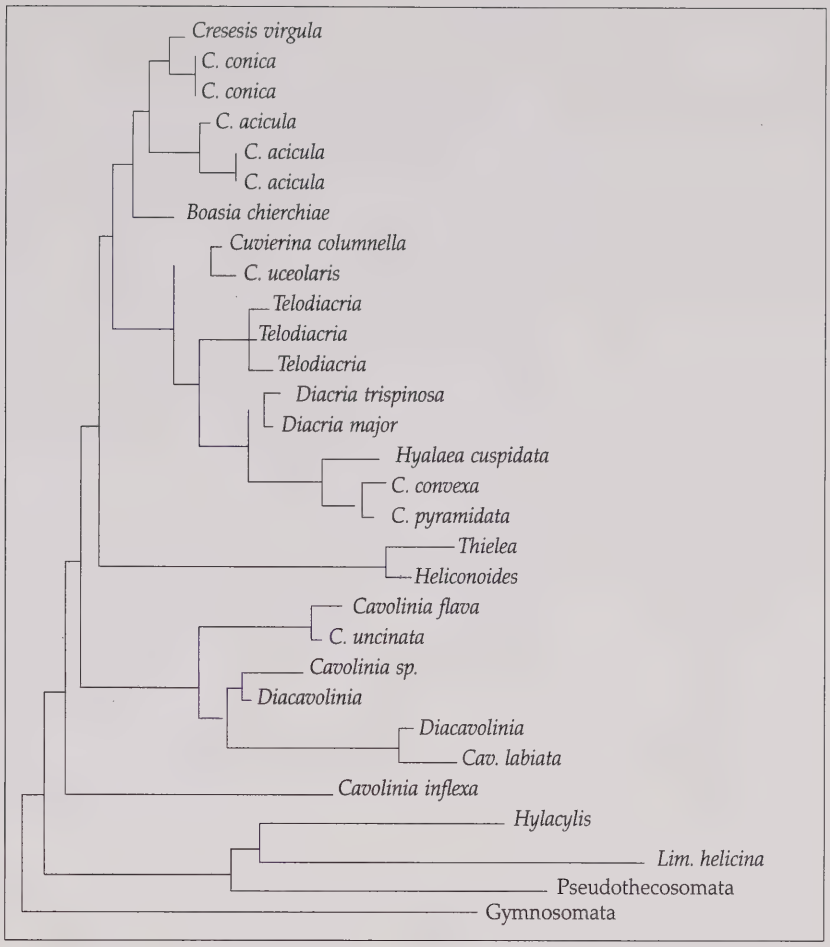

Fig. 16. Schematic phylogenetic tree of Euthecosomata (COI data) (original tree in Corse et al., 2013).

Fig. 16. Albero filogenetico schematico degli Euthecosomata (dati COI) (albero originale in Corse et al., 2013).

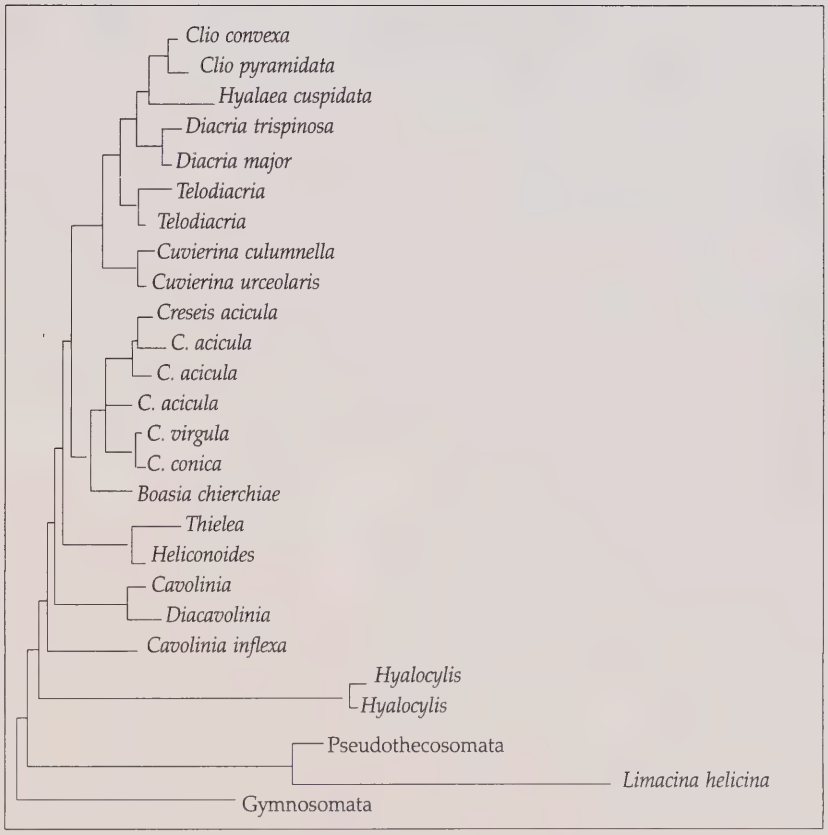

Fig. 17. Schematic phylogenetic tree of Euthecosomata in COI data set (original tree in Corse et al., 2013).

Fig. 17. Albero filogenetico schematico degli Euthecosomata nella serie di dati COI (albero originale in Corse et al., 2013).

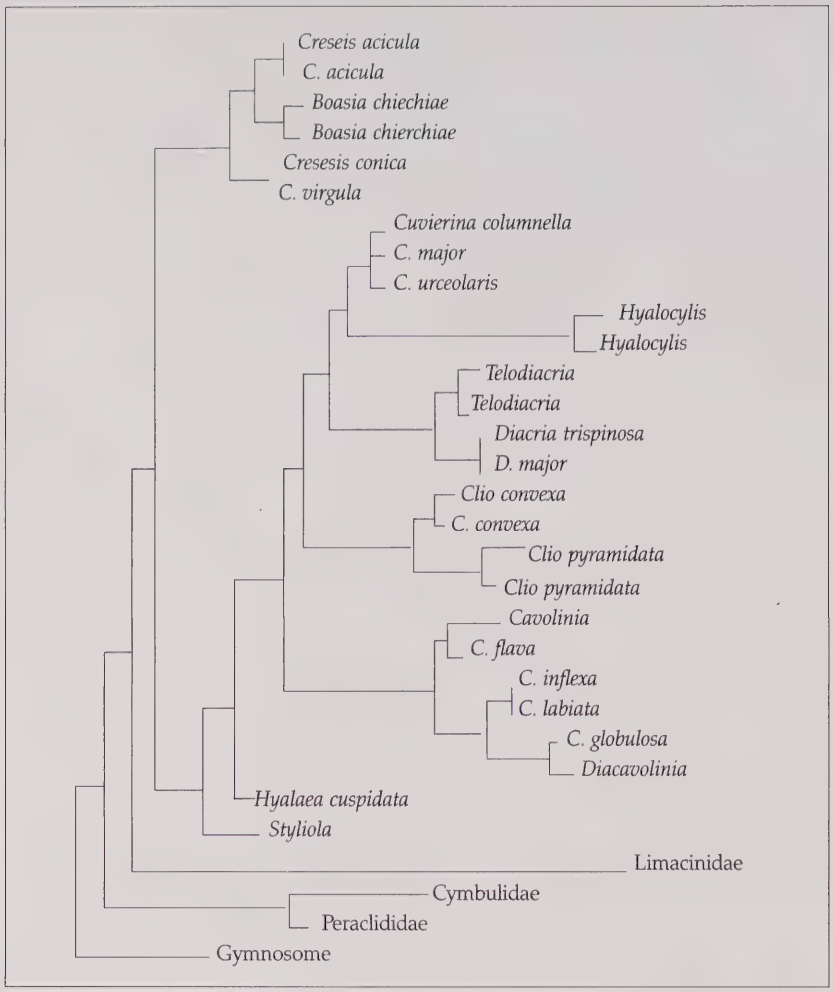

Fig. 18. Schematic Phylogenetic tree of Euthecosomata (28S molecular data) (original tree in Corse et al., 2013).

Fig. 18. Albero filogenetico schematico degli Euthecosomata (dati molecolari 28S) (albero originale in Corse et al., 2013).

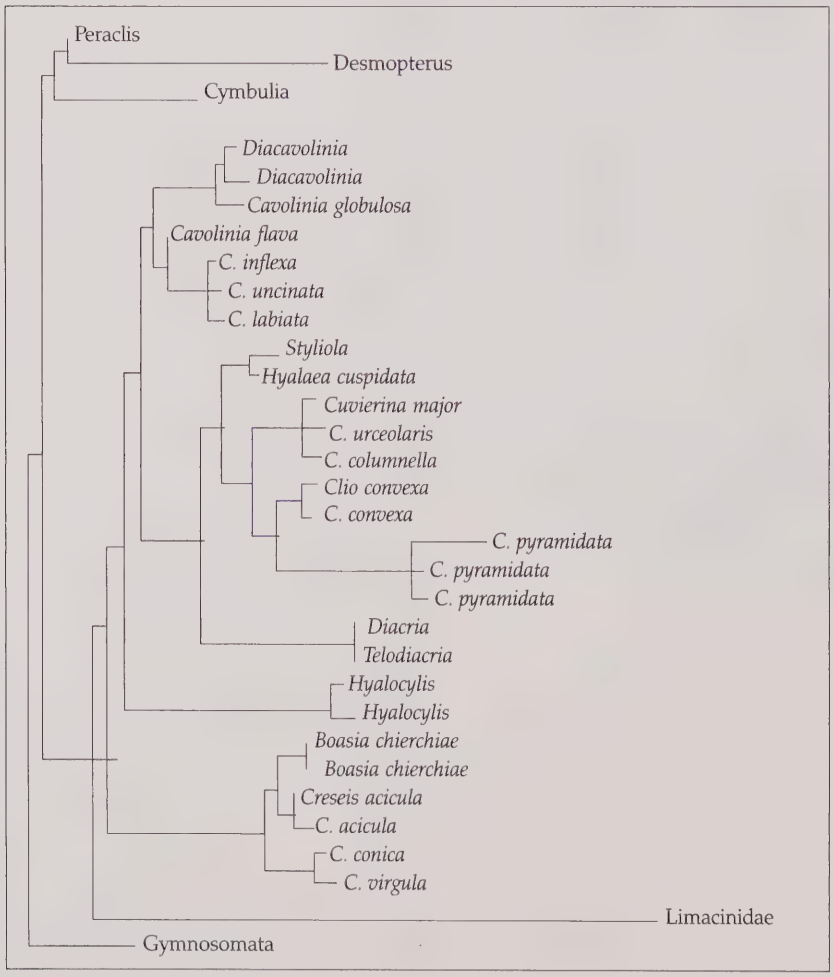

Fig. 19. Schematic phylogenetic tree of Euthecosomata in 28S gene data set (original tree in Corse et al., 2013).

Fig. 19. Albero filogenetico schematico degli Euthecosomata nella serie del gene 28S (albero originale in Corse et al., 2013).

References

Abildgaard P.C., 1791. Nyere efterretning om det skaldyr fra middelhavet, form Forskal Harbeskrevet under navn of *Anomia tridentata. Skrivter Naturhistorie-Selskabet*, Kobenhavn, **1** (2): 171-175.

Almoggi-Labin A., 1882. Stratigraphic and paleoceanographic significance of late Quaternary pteropods from deep-sea cores in the Gulf of Aqaba (Elat and northern most Red Sea. *Marine Micropaleontology*, **7** (1): 53-72.

Bandel K., 1977. Die Herausbildung der Schraubenschicht der Pteropoden. *Biomineralization Research Reports*, **9**: 73-85.

Bandel K., Almogi-Labin A., Hemleben C. & Deuser W.G., 1984. The conch of *Limacina* and *Peraclis* (Pteropoda) and a Model for the Evolution of Planktonic Gastropods. N. *Jb. Geological Paläontology Abh.*, **168** (1): 87-107.

Bandel K. & Hemleben C., 1995. Observations on the ontogeny of Thecosomatous Pteropods (holoplanktonic Gastropoda) in the Southern Red Sea and from Bermuda. *Marine Biology*, **124** (2): 225-243.

Be A. W.H., Mac Clintock C. & Currie D.C., 1972. Helical shell structure and growth of the pteropod *Cuvierina columnella* (Rang) (Mollusca, Gastropoda). *Biomineralisation Research Reports*, **4**: 47-79.

Be A.W.H. & Gilmer R.W., 1977. A zoogeographic and taxonomic review of Euthecosomatous Pteropoda. *Oceanic Micropaleontology*, **1** (6): 733-808.

Berggren W.A., Kent D.V., Swisher C.C., Aubry M-P, 1995. A revised Cenozoic geochronology and chronostratigraphy. *SEPM*, **54**: 138-144.

Blainville M.H. De, 1821. Hyale, *Hyalaea* (Malacozoa). *Dictionnaire de Sciences naturelles*, **22**: 65-83.

Blainville M.H. De, 1816-1824. *Dictionnaire des Sciences naturelles*. Paris & Strasbourg, 1-567.

Bleeker J. & Spoel S. van der, 1988. *Diacria piccola* and *Diacria maculata* two new Pteropod mollusc species from the Atlantic and Pacific oceans. *Proceedings of the Biological Society of Washington*, **101** (1): 60-66.

Boas J.E.V., 1886. Spolia Atlantica. Bidrag til Pteropodernes. Morfology og Systematik sampt til Kunds Kaben om deres geografiske Udbredelse. *Videnskabernes Selskabs Skrifter 6 Raekke, Naturvidenskabeling Mathematik Afdeling*, **4** (1): 1-231.

Bonnevie K., 1913. Pteropoda. *Reports on the Scientific Results of the 'Michael Sars' North Atlantic deep Sea Expedion 1910*, **3** (1): 1-59.

Bontes B. & Spoel S. van der, 1998. Variation in the *Diacria trispinosa* group, new interpretation of colour patterns and description of *D. rubecula* n. sp. (Pteropoda). *Bulletin Zoologisch Museum Universiteit van Amsterdam*, **16**: 77-84.

Bosc L.A.G., 1802. *Histoire naturelle des coquilles contenant leur description, les moeurs des animaux qui les habitent et leurs usages*. Deterville, Paris, 1-330.

Bosc L.A.G., 1816 -1817. *Nouveau dictionnaire d'Histoire Naturelle*. Deterville, Paris, 1-592.

Bouchet P., Rocroi J.-P., Hausdorf B., Kaim A., Kano Y., Nützel A., Parkhaev P., Schrödl M. & Strong E., 2017. Revised classification, nomenclator and typification of Gastropod and Monoplacophoran families. *Malacologia*, **61** (1-2): 1-526.

Burridge A.K., Goetze E., Raes N., Huisman J. & Peijnenburg K., 2015. Global geography and evolution of *Cuvierina* pteropods. *BMC Evolutionary Biology*, **15**: 1-16.

Burridge A.K., Janssen A.W., Katja T.C.A. & Peijnenburg K., 2016. Revision of the genus *Cuvierina* Boas, 1886 based on integrative taxonomic data, including the description of a new species from the Pacific Ocean (Gastropoda, Thecosomata). *ZooKeys*, **619**: 1-12.

Cahuzac B. & Janssen A.W., 2010. Eocene to Miocene holoplanktonic Mollusca (Gastropoda) of the Aquitaine Basin, southwest France. *Scripta geologica*, **141**: 1-193.

Cantraine F., 1841. Malacologie Méditerranéenne et littorale. *Memoire de l'Académie Royale de Bruxelles*, **13**: 1-173.

Chen C. & Be A.W.H., 1964. Seasonal distribution of Euthecosomatous Pteropos in the surface waters of five stations in the western North Atlantic. *Bulletin of Marine Science of the Gulf and Caribbean*, **14** (2): 185-220.

Corse E., Rampal J., Cuoc C., Pech N., Perez Y. & Gilles A., 2013. Phylogenetic Analysis of Thecosomata Blainville, 1824 (Holoplanktonic Opisthobranchia) Using Morphological and Molecular Data. *PLOS ONE* 8: **e5943**: 1-20.

Croce N. della & Frontier S., 1966. Thecosomatous pteropods from the Mozambique channel. *Bollettino Museo Instituto Biologia Università Genova*, **34** (207): 107-113.

Curry D., 1965. The English Paleogene Pteropods. *Procceding of the Malacological Society of London*, **36**: 357-371.

Curry D., 1981. Ptéropodes Eocènes de la tuileris de Gan (Pyrénées-Atlantiques) et de quelques autres Localités du SW de la France. *Cahiers de Micropaléontologie*, **4**: 35-44.

Curry D. & Rampal J., 1979. Shell microstructure in fossil Thecosome Pteropods. *Malacologia*, **18**: 23-25.

Dall W.H., 1889. A preliminary catalogue of the shell bearing marine mollusks and brachiopods of the south-eastern Coast of the United States, with Illustrations of many of the species. *Bulletin of United States National Museum*, **37**: 3-221.

Dall W.H., 1921. Summary of the marine shell bearing mollusks of the North West Coast of America from San Diego, California of the polar sea, mostly contained In the collection of the United States National Museum with Illustrations of hiterto unfigured species. *Smithsonian Institut U.S. Natural Museum Bulletin*, **112**: 1-217.

Dall W.H. & Simpson C.T., 1900. The Mollusca of Porto Rico. *Bulletin of U.S. Fish Commission* ? (1): 353-524.

Daumas R. & Ceccaldi H.J., 1965. Contribution à l'étude biochimique d'organismes marins. 1- Acides aminés libres et proteiques chez *Beroe ovata* (Eschscholtz), *Ciona intestinalis* L.), *Cymbulia peroni* (De Blainville) et *Rhizostoma pulmo* (Agassiz). *Travaux de la Station Marine d'Endoume*, **38** (54): 3-14.

Dayrat B., Tillier A., Lecointre G. & Tillier S., 2001. New clade of Euthyneuran Gastropods (Mollusca) from 28S rRNA Sequences. *Molecular Phylogenetics and Evolution*, **19** (2): 225-235.

Deshayes G.P. & Milne Edward H., 1836. in Lamarck, J.B. *Histoire naturelle des animaux sans vertèbres*. J.B. Baillière, Paris 2e ed. 7, 1-736.

Dupont L., 1979. Note on variation in *Diacria* Gray, 1847, with desriptons of a species new to science, *Diacria rampali* nov. spec. and a forma new to science, *Diacria trispinosa* forma *atlantica* nov. forma. *Malacologia*, **18**: 37-52.

Fol H., 1875. Sur le développement des Ptéropodes. *Archives de zoologie expérimentale générale*, **4** (1): 1-214.

Forbes E., 1844. Report on the Mollusca and Radiata of the Aegean Sea and on their distribution considered as bearing on geology. *Report of the 13th Meeting of the Britisch Association for the Advancement of Science 1843*: 131-193.

Frontier S., 1963. Hétéropodes et Ptéropodes récoltés dans le plancton de Nosy-Bé. *Cahiers O.R.S.T.O.M. Série Océanographie*, **6**: 213-227.

Frontier S., 1965. Le problème de *Creseis*. *Cahiers O.R.S.T.O.M. série océanographie*, **3** (2): 11-17.

Gasca R. & Janssen A.W., 2013. Taxonomic review, molecular

data and key to the species of Creseidae from the Atlantic Ocean. *Journal of Molluscan Studies*, ?: 1-8.

Glaçon G., Rampal J., Gaspard D., Guillaumin D. & Scott Staerker T., 1994. 15. Thecosomata (Pteropods) and their remains in late quaternary deposits on the Bougainville Guyot and the Central New Hebrids Island Arc. *Proceeding of Oceaographical Drill Programme Science Research*, **134**: 319-334.

Gray J.E., 1840. *Synopsis of the contents of the British Museum.* 41st Ed. G. Woodfall, London, 106-156.

Gray J.E., 1847. A list of the Genera of Recent Mollusca, their Synonyma and Types. *Proceeding of the Zoological Society of London*, **15**: 129-219.

Gray J.E., 1850. *Catalogue of the Mollusca in the Collection of the British Museum.* Part II Pteropoda. E. Newman London, 1-45.

Haszprunar G., 1985. The Heterobranchia a new concept of the phylogeny of the higher Gastropoda. *Sond. Z.-f. zoological Systematic Evolution forschung*, **23**: 15-37.

Hedley C., 1917. A Checklist of the marine fauna of New South Wales. Part. I. *Proceeding of the Royal Society New South Wales* (1917) 51: 1-120.

Herrmannssen A.N., 1846-1849. *Indicis Generum Malacozoorum Primordia.* Kassel 1, 2: 637 pp. (1846): 717 pp. (1847-1849).

Hodgkinson K.A., Garvie C.L. & Be A.W.H., 1992. Eocene Euthecosomatous Pteropoda (Gastropoda) of the Gulf and Eastern Coast of North America. *Bulletin of American Paleontology*, **103** (341): 1-62.

Hoffman H., 1939. *Opisthobranchia* In: bronns H.G. ed. Klassen und Ordnungen des Tierreichs. Akademischer Verlag. Leipzig, **3** (2): 219-1118.

Huber G., 1993. On the cerebral nervous system of marine Heterobranchia (Gastropoda). *Journal of Molluscan Studies*, **59**: 381-420.

Hunt B., Stugnell J., Bednarsek N., Linse K., Nelson R. J., Pakhomov E., Seibel B., Steinke D. & Wûrzberg L., 2010. Poles Apart: "Bipolar Pteropod Species *Limacina helicin* Is Genetically Distinct between the Arctic and Antarctic Oceans. *PLOS ONE*, **5** (3): e9835/ 1-4.

International Commission on Zoogical Nomenclature, 1999. *International Code of Zoological Nomenclature.* Fourth edition. The International Trust for Zoological Nomenclature, London, 1-306.

Issel A., 1869. *Malacologia des Mar Rosso.* Biblioteca di Malacologia, Pisa, 1-387.

Janssen A.W., 2003. Notes on systematics, morphology and biostratigraphy of fossil holoplanktonic Mollusca, 13. Considerations on a division of Thecosomata, with the emphasis on genus group classification of Limacinidae. *Caenozoic Research*, **2**: 163-170.

Janssen A.W., 2004. Holoplanktonic molluscan assemblages (Gastropoda, Heteropoda, Thecosomata) from the Pliocène of Estepona (Spain, Malaga). *Palaeontos*, **5**: 103-131.

Janssen A.W., 2005. Development of Cuvierinidae (Mollusca Euthecosomata, Cavolinioidea) during the Caenozoic: a non-cladistic approach with a re-interpretation of recent taxa. *Basteria*, **69**: 25-72.

Janssen A.W., 2012. Systematics and biostratigraphy of holoplanktonic Mollusca from the Oligo-Miocene of the Maltese Archipelago. *Bolletino del Museo Regionale di Scienze Naturali*, **28** (12): 197-601.

Janssen A.W., Jagt J.W.M., Yazdi M., Bahrami A., Sadri S., 2013. Early-middle Eocene faunal assemblages from the Soh area, north-central Iran, 1. Introduction and pteropods (Mollusca, Gastropoda, Thecosomata). *Cainozoic Research*, **10** (1-2): 23-34.

Janssen A.W., 2018. The status od *Cuvierina spoeli* Rampal, 2002 and Cuvierna oryza *Benson*, 1835 (Gastropoda, Pteropoda, Cuvierinidae). *Zootaxa*, **4459** (2): 369-375.

Janssen A.W., 2018. Note on the systematics, morphology, biostratigraphy of holoplanktonic Mollusca, 25. Once more: The correct name for the type species of the genus *Creseis* Rang, 1828 (Pteropoda, Euthecosomata, Creseidae) *Basteria*, **82** (4-6): 1-3.

Jeffreys J.G., 1869. *Britisch Conchology.* J.v. Voorst, London, **5**: 1-258.

Jeffreys J.G., 1877. New and peculiar Mollusca of the Eulimidae and other families of Gastropoda, as well as the Pteropoda, procured in the "Valorous" expedition. *Annales Mag. natural History*, **19** (4): 317-339.

Jennings R.M., Bucklin A., Ossenbrugger H. & Hopcroft R., 2010. Species diversity of planktonic gastropods (Pteropoda and Heteropoda) from six ocean regions based on DNA barcodes analysis. *Deep-Sea Research Part II Oceanography*, **57**: 2199-2210.

Johnson C.W., 1934. List of marine Molluscs of the Atlantic coast from Labrador to Texas. *Proceeding of the Boston Society Natural History*, **40** (1): 1-204.

Klussmann-Kolb A. & Dinapoli A., 2006. Systematic position of the pelagic Thecosomata and Gymnosomata within Opisthobranchia (Mollusca, Gastropoda), revival of Pteropoda. *Journal of zoological Systematic Evolution Research*, **44** (2): 118-129.

Lalli C.M. & Wells F.E., 1973. Brood protection in an epipelagic thecosomatous pteropod, *Spiratella* (*'Limacina'*) *Inflata* (d'Orbigny). *Bulletin of the Marine Science*, **23** (4): 933-941.

Lalli C.M. & Gilmer R.W., 1989. *Pelagic snails. The biology of holoplanktonic gastropod mollusks.* Stanford Univ. Press, Stanford, 1-259.

Lemche H., 1948. Northern and Arctic techtibranch gastropods. *K. danske Videnskabernes Selskabs Skrifter* **5**:1-136.

Linnaeus C., 1767. *Systema naturae.* Editio duodecima reformata Salvii, Holmiae, 533-1327.

Maas A.E., Blanco-Bercial L. & Lawson G., 2013. Reexamination of the species Assignment of *Diacavolinia* Pteropods using DNA Barcoding. PLOS ONE, **8** (1): e 53889.

Massy A.L., 1909. The Pteropoda and Heteropoda of the coast of Ireland. Fisheries, Ireland Scientific Investigations (1907). II. *Department of Agriculture and Technological Instruction for Ireland*: 1-52, pl. 1.

Massy A.L., 1920. Eupteropoda (Pteropoda Thecosomata) and Pterota (Pteropoda Gymnosomata). *British ("Terra Nova") Expedition 1910, Natural History Report, Zoology* II (9), (Mollusca 3): 203-232.

May W.L., 1921. *A check-list of the Mollusca of Tasmania.* John Vail, Tasmania, 1-114.

Mc Gowan J.A., 1960. *The systematics, distribution and abondance of Thecosomata of the North Pacific.* Unpubl. D. Thesis University of California at San Diego: 1-197.

Meisenheimer J., 1905a. Pteropoda. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer Valdivia* 1898-1899, **9** (1): 1-314.

Meisenheimer J., 1905 b. Die Arktischen Pteropoden. *Fauna Arctica*, **4** (II). G. Fischer, Jena: 407-430.

Meisenheimer J., 1906. Die Pteropoden der deutschen Süd-Polar Expedition 1901-1903. *Deutschen Süd-Polar Expedition 1901-1903* (Zoology), **1** (2): 92-152.

Menzies R.J., 1958. Shell-bearing pteropods from Mediterranean plankton (Cavoliniidae). *Pubblicazione Stazione Zoologica Napoli*, **30** (3): 381-401.

Monterosato M. di, 1878. Enumerazione e sinonimia delle conchiglie Mediterranee. *Giornale di Scienza Naturale ed Economica Palermo*, **13** (14): 61-115.

Monterosato M. di, 1884. *Nomenclature generica e specifica di alcune conchiglie Mediterranee.* Palermo Stabilmento Tipografico Virzì: 1-152.

Mörch O., 1850. *Catalogus Conchyliorum quae reliquit.* C. P. Kierult MD. DR. Typis Triery, Hafniae dividenda: 1-33.

Morton J.E., 1946. The biology of *Limacina retroversa. Journal of Marine Biological Association of the United Kingdom,* **33**: 297-312.

Morton J.E. 1958. - Observation on the gymnosomatous pteropod *Clione limacina* (Phipps). *Journal of Marine Biological Association of the United Kingdom* 37: 287-297.

Odhner J. 1939. - Opisthobranchiate Mollusca from the western and northern coast of Norway. *K. Nor Videnskabernes Selskabs Skriifter* 1: 1-93.

Orbigny A.d', 1834-1847. *Voyage dans l'amérique Méridionale Exécuté pendant les Années 1826-1833. Mollusques.* Bertrand & Levrault Paris, **5** (3): 49-184; Atlas: pls 1-85.

Pelseneer P., 1888. Report on the Pteropoda collected by H.M. S. Challenger during the years 1873-1876. II. The Thecosomata. *Reports on the Scientific Results of the Voyage of H. M. S. Challenger during 1873-1876,* **23** (1): 1-132.

Pfeffer G., 1880. Die Pteropoden des Hamburger Museums. *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg,* **7**: 69-99.

Phipps C.J., 1774. *A voyage towards the North Pole understaken by his Majesty's Command 1773.* Bowyer and Nichols London: 1-275.

Phipps C.J., 1775. *Voyage au pôle boreal fait en 1773.* Saillany, Nyon and Pissot Paris 1-12: 1-261.

Poulicek M., Voss-Foucard M.-F. & Jeuniaux C., 1991. - Regressive shell evolution among Opisthobranch Gastropods. *Malacologia,* **32** (2): 223-232.

Pruvot-Fol A., 1954. Mollusques Opisthobranches. *Faune de France,* **58**: 1-457.

Quoy J.R.C. & Gaimard J.P., 1827. Observations zoologiques faites à bord de L'Astrolabe en mai 1926, dans le détroit de Gibraltar: description des genres Biphore, Carinaire, Hyale, Flèche, Cleodore, Anatife et Briarée. *Annales de Sciences Naturelles,* **10**: 225-239.

Rampal J., 1964. Etude de l'opercule de *Spiratella* (*Limacina*) *inflata* (d'Orbigny, 1836). *Bulletin de*
l'Institut Océanographique de Monaco 61 (1285): 1-12.

Rampal J., 1965a. Pteropodes indicateurs hydrologiques. *Revue des Travaux de l'Institut des Pêches maritimes,* **29** (4): 393-400.

Rampal J., 1965b. Variations morphologiques au cours de la croisance d'*Euclio cuspidata* (Bosc).
Bulletin de l'Institut Océanographique de Monaco, **65** (1360): 1-12.

Rampal J., 1966. Pêches planctoniques superficielles et profondes en Méditerranée occidentale (Campagne de la «Thalassa» - Janvier 1961 -entre les îles Baléares, la Sardaigne et l'Algérois). VI. Ptéropodes. *Revue des Travaux de l'Institut des Pêches maritimes,* **30**: 375-383.

Rampal J., 1967. Répartition quantative et bathymétrique des Ptéropodes Thécosomes récoltés en Méditerranée occidentale au nord du 40e parallèle. Remarques morphologiques sur certaines espèces. *Revue des Travaux de l'Institut des Pêches maritimes,* **31** (4): 403-416.

Rampal J., 1970a. Ptéropodes Thécosomes indicateurs d'eau d'influence atlantique en Méditerranée. *Journées Etudes planctonologiques. Rapports de la Commission internationale Mer Méditerranée*: 45-48.

Rampal J., 1970b. Ptéropodes Thecosomes indicateurs d'eau d'origine orientale en Méditerranée occidentale. *Journées Etudes Planctonologiques. Rapports de la Commission Internationale Mer Méditerranée*: 49-52.

Rampal J., 1972. Structure de la coquille des Ptéropodes au microscope à balayage. *Rapports de la Commission internationale Mer Méditerranée, 23e Réunion Assemblée plénière, Comité Plancton,* Athènes, 1972.

Rampal J., 1973. Phylogénie des Ptéropodes Thécosomes d'après la structure de la coquille et la morphologie du manteau. *Compt-Rendu Académie des Sciences de Paris,* **277**, sér. D: 1345-1348.

Rampal J., 1974. Structure de la coquille des Ptéropodes au microscope à balayage. *Rapports de la Commission internationale mer Méditerranée,* **22** (9): 133-134.

Rampal J., 1975. *Les Thécosomes (Mollusques pélagiques). Systématique et Evolution. Ecologie et Biogéographie méditerranéennes.* Thèse Doctorat d'Etat, Université de Provence Aix-Marseille II, c. n. r. s. ao 11932: 1-485.

Rampal J., 1979. Thécosomes tropicaux dans les sédiments de la mer Tyrrhénienne. *Rapports de la Commission internationale Mer Mediterranée* **25/26** (8):149-150.

Rampal J., 1985. Systématique du genre *Creseis* (Mollusques, Thécosomes). *Rapports de la Commisson internationale Mer Mediterranée,* **29** (9): 259-253.

Rampal J., 1990a. A propos des migrations lesseptiennes. Les Thecosomes de la mer Rouge. *Bulletin de l'Institut océanographique,* Monaco, n° spécial, **7**: 103-107.

Rampal J., 1990b. La campagne MD 50/JASUS aux Îles Sain-Paul et Amsterdam à bord du «MARION DUFRESNE» 03 07 -01 08 1986. Rapports de la campagne en mer, n° 86-04: 77-78.

Rampal J., 1996. *Clio oblonga* n. sp. (Mollusque Gastéropode, Euthécosome, Cavoliniidae, Clionae) fossile de thanatocoenoses quaternaires de la Méditerranée. *Géologie Méditerranéenne,* **23** (3-4): 175-185.

Rampal J., 2002. Biodiversité et biogéographie chez les Cavoliniidae (Mollusca, Gastropoda, Opisthobranchia, Euthecosomata). Régions faunistiques marines. *Zoosystema,* **24** (2): 209-258.

Rampal J., 2011. Clés de détermination des Thecosomata (Pteropoda) (Mollusca Opisthobranchia Holoplanctoniques) de Méditerranée et de l'Atlantique Eurafricain. *Revue des Travaux de l'Institut des Pêches maritimes,* **37** (3): 369-389, 1973 révisé en 2011.

Rampal J., 2014. *Cavolinia gibbosa* group (Holoplanktonic Opisthobranchia, Euthecosomata): systematics and problems of synonymy (comment on Arie W. Janssen, 2012). *Bolletino Malacologico,* **50**: 1-10.

Rampal J., 2017. Euthecosomata (Mollusca, Gastropoda, Thecosomata) Taxonomic Review. BIORXIV-2017-098475v1: 1-80.

Rang P.C.A.L., 1827. Description de 2 genres nouveaux (Cuvieria et Euribia) appartenant à la classe des Pteropodes. *Annales de Sciences Naturelles,* **12**: 320-329.

Rang P.C.A. L., 1828. Notice sur quelques mollusques nouveaux appartenant au genre cléodore et établissement et monographie du sous-genre creseis. *Annales de Sciences Naturelles* 13: 302-319.

Rang P.C.A.L., 1829. *Manuel de l'histoire naturelle des Mollusques et de leurs coquilles.* Roret, Paris: 1-390.

Rang P.C.A.L. &. Férussac D. de, 1830. Uber die Pteropoden und andere Mollusken. *Notizen aus dem Gebiete der Natur und Heilkunde,* **26** (16): 260-262.

Richter G., 1973. Zur Stammeschichte pelagischer Gastropoden. *Naturmuseum Frankfurt am Main,* **103** (8): 265-275.

Richter G., 1976. Zur Frage der Verwandtschaftsbeziehungen von Limacinidae und Cavoliniidae (Pteropoda: Thecosomata). *Archiv für Mollusken kunde Frankfort am Main,* **107** (1/3): 137-144.

Sakthivel M., 1974. A new species of *Creseis* (Gastropoda,

Mollusca) from the Laccadive Sea. *Current Science*, **43** (19): 619-620.

Salvini-Plawen L., 1970. Zur systematischen Stellung von *Soleolifera* und *Rhodope* (Gastropoda, Euthyneura). *Zoological Journal of Systematic*, **97**: 285-299.

Schiemenz P., 1906. Die Pteropoden der Plankton Expedition. *Ergbenisse der Nord-Atlantic. Plankton Expedition der Humboldtstiftung, Kiel und Leipzig*, **2**: 1-37.

Souleyet F.L.A., 1851. Ordre des Ptéropodes. *Journal de Conchyliologie*, **2**: 29-38.

Souleyet F.L.A., 1852. *In* Rang P.C.A.L. & Souleyet F.L.A. - *Histoire naturelle des mollusques ptéropodes. Monographie comprenant la description de toutes les espèces.* Baillière, Paris: 1-86.

Spoel S. van der, 1963. A new forma of the species *Clio pyramidata Linnaeus*, 1767 and a new resting stage of *Clio pyramidata* forma *sulcata* Pfeffer (1879) (Gastropoda Pteropoda). *Beaufortia*, **10** (114): 19-28.

Spoel S. van der, 1964. Notes on some Pteropods from the North Atlantic. *Beaufortia*, **10** (121): 167-176.

Spoel S. van der, 1967. *Euthecosomata a group with remarkable developmental stages (Gastropoda, Pteropoda).* J. Noorduijn Gorinchem: 1-375.

Spoel S. van der, 1969a. The shell of *Clio pyramidata* L., 1767 forma *lanceolata* (Lesueur, 1813) and forma *convexa* (Boas, 1886) (Gastropoda, Pteropoda). *Vidensk Meddel fra Dansk Naturhist Forening*, **133**: 95-114.

Spoel S. van der, 1969b. Two new forma of *Cavolinia uncinata* (Rang, 1829) (Pteropoda, Gastropoda). *Basteria*, **16** (121): 185-198.

Spoel S. van der, 1970a. Morphometric data on Cavoliniidae, with notes on a new form of *Cuvierina columnella* (Rang, 1827) (Gastropoda, Pteropoda). *Basteria*, **34** (5-6): 103-150.

Spoel S. van der, 1970b. The pelagic Mollusca from the "Atlantide" and "Galathea" expeditions collected in the East Atlantic. *Atlantide Reports*I, **2**: 99-139.

Spoel S. van der, 1971. New forms of *Diacria quadridentata* (de Blainville, 1921); *Cavolinia longirostris* (de Blainville, 1821) and *Cavolinia uncinata* (Rang, 1829) from the Red Sea and the East Pacific Ocean (Mollusca, Pteropoda). *Beaufortia*, **19** (243): 1-20.

Spoel S. van der, 1973. Variation in *Cavolinia longirostris* (de Blainville, 1821) from the Pacific Ocean with description of a new forma (Mollusca, Gastropoda). *Bulletin Zoölogisch Museum, Universiteit van Amsterdam*, **3** (14): 99-101.

Spoel S. van der, 1974. Geographical variation in *Cavolinia tridentata* (Mollusca, Pteropoda). *Bijdragen tot de dierkunde*, **44** (1): 99-112.

Spoel S. van der, 1976. *Pseudothecosomata, Gymnosomata and Heteropoda (Gastropoda)*. Bohn, Scheltema & Holkema, Utrecht: 1-484.

Spoel S. van der, 1987. *Diacavolinia* nov. gen. separated from *Cavolinia* (Pteropoda, Gastropoda). *Bulletin Zoöllogisch Museum, Universiteit van Amsterdam*, **11**: 77-79.

Spoel S. van der, Schalk P.H. & Bleeker J., 1992. *Clio piatkowskii* a mesopelagic Pteropod new to Science (Gastropoda, Opisthobranchia). *Beaufortia*, **43** (1): 1-6.

Spoel S. van der, Bleeker J. & Kobayasi H., 1993. From *Cavolinia longirostris* to twenty-four *Diacavolinia* taxa, with a phylogenetic discussion (Mollusca, Gastropoda). *Bijdragen tot de Dierkunde*, **62**: 127-166.

Squires R.L., 1989. Pteropods (Mollusca, Gastropoda) from Tertiary formations of Washington and Oregon. *Journal of Paleontology*, **63** (4): 443-448.

Strebel H., 1908. Die Gastropoden. *Wissenschaftliche Ergebnissen Schwed Südpolar Expedition 1901-1903*, **6** (1): 1-111.

Steur A., 1911. Adriatische Pteropoden. *Sitzung Berichte der Mathematisch-Naturwissen-schaftlichen Klasse Akademie der Wissenschften in Wien*, **130** (I): 1-22.

Tesch J.J., 1913. *Pteropoda*. In: F.E. Schulze. Das Tierreich (herausgegeben von), R. Friedländer and S., Berlin, **36**: 1-154.

Tesch J.J., 1946. The Thecosomatous Pteropods. I. The Atlantic. *Dana Report*, **5** (28): 1-82.

Tesch J.J., 1948. The Thecosomatous Pteropods. II. The Indo-Pacific. *Dana Report*, **5** (30): 1-45.

Ujihara A., 1996. Pteropods (Mollusca, Gastropoda) from the Pliocene. Miyazaki group, Miyazaki Prefecture, Japan. *Journal of Paleontology*, **70** (5): 771-788.

Vayssiere A., 1915. Mollusques Euptéropodes (Ptéropodes Thécosomes) provenant des Campagnes des yachts'Hirondelle' et 'Princesse Alice' (1885-1913). *Résultats des Campagnes Scientifiques accomplies sur son yacht par Albert 1er Prince souverain de Monaco*, **47**: 3-226.

Vives F., 1966. Zooplankton neritico de las aguas de Castellan (Mediterraneo occidental). *Investigaciones Pesqueras*, **30**: 49-166.

Wägele H., Klussmann-Kolb A., Verbeek E. & Schrödl M., 2013. Flashback and foreshadowing- a review of the taxon Opisthobranchia. *Org. Diversity Evolution* DOI 10. 1007/ s13127-013-0151-5.

Watelet A. & Lefevre T., 1885. - Note sur des Ptéropodes du genre *Spirialis* découverts dans le Bassin de Paris. *Société Malacolologique Belgique*, **15**: 100-103.

Wellls F.E., 1976. Seasonal Patterns of Abondance and Reproduction of Euthecosomatous Pteropoda off Barbados, West Indies. *Veliger*, **18**: 241-248.

Wells F.E., 1978. Subgeneric relationships in the Euthecosomatous Pteropod genus *Limacina* Bosc, 1817. *Journal of Malacological Society Australia*, **4** (1-2): 1-5.

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Subfamily Cardiinae Lamarck, 1809
Genus *Acanthocardia* Gray, 1853
(type species *Cardium aculeatum* Linné, 1758)

Cardium indicum Lamarck, 1819
(Fig. 1. A-D, Fig. 2. C)

Cardium hians Brocchi, 1814: p. 508, tav. 13, fig. 6 (non Spengler, 1799).
Cardium indicum Lamarck, 1819: p. 4.
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Esempi di bibliografia:
Salas C., 1996. Marine Bivalves from off the Southern Iberian Peninsula collected by the Balgim and Fauna 1 expeditions. *Haliotis*, **25**: 33-100.
Grill B. & Zuschin M., 2001. Modern shallow- to deep-water bivalve death assemblages in the Red Sea - ecology and biogeography. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **168**: 75-96.
Boss K.J., 1982. Mollusca, in Parker S.P. (ed.), *Synopsis and Classification of Living Organisms*. Vol. 1. McGrow-Hill, New York: 945-1166.
Carter J.G., Campbell D.C. & Campbell M.R. 2000. Cladistic perspectives on early bivalve evolution, in Harper E.M., Taylor J.D. & Crame J.A. (eds), The Evolutionary Biology of the Bivalvia. *Geological Society, London, Special Publications*, **177**: 47-95.
Vokes H.E., 1980. *Genera of the Bivalvia: a systematic and bibliographic catalogue (revised and update)*. Paleontological Research Institution, Ithaca, Edwards Brothers Inc., 307 pp.

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Le illustrazioni devono essere di alta qualità, in formato elettronico (.tiff), con una risoluzione non più bassa di 300 dpi per le fotografie e di 600 dpi per i disegni ed i grafici. Vanno preparate alle esatte dimensioni di stampa, in formato colonna singola (8,4 cm) o colonna doppia (17,2 cm). L'area di stampa massima è 17,2 × 26,5 cm. La dimensione delle illustrazioni va scelta con attenzione e buon senso, sulla base della complessità e quantità delle immagini contenute, al fine di ovviare a risultati scientificamente poco utili ed esteticamente poveri, oltre allo spreco di spazio di stampa.
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Le illustrazioni vanno citate nel testo come figure, usando le abbreviazioni **Fig.** e **Figg.** come nell'esempio: **Fig. 3, Fig. 6. A-F, Fig. 5. A, 7. B, Figg. 3, 5**. Le illustrazioni in altri lavori vanno citati come fig. o figg.
Le immagini, montate su fondo nero o bianco, devono avere dimensioni adeguate ad un'agevole lettura, non più piccole di 4-5 cm, né eccessivamente grandi. Devono essere appropriatamente disposte nello spazio disponibile, in modo da evitare ampie aree vuote. Lineette di scala, nere o bianche, possono essere applicate sulle illustrazioni.
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Le illustrazioni vanno tenute separate dal testo. La pubblicazione di illustrazioni a colori deve essere preliminarmente accordata con il Direttore Scientifico. Gli originali delle illustrazioni vanno spediti solo dopo l'accettazione definitiva del manoscritto.

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Le tabelle vanno composte come files di testo, esattamente alla dimensione di stampa (si veda Illustrazioni), con un carattere *sans-serif* non più piccolo di 8-9 punti. Vanno evitati bordi spessi e griglie eccessivamente pesanti. Le tabelle sono citate nel testo come Tab. (es.: **Tab. 2**, **Tabb. 3-6**). Le abbreviazioni vanno spiegate in didascalia o nei Materiale e metodi. Le tabelle non vanno inserite nel testo, ma salvati come files separati.

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Le didascalie vengono riportate in una parte distinta del manoscritto, raggruppate ed in sequenza. Devono comprendere: nome ed autore della specie illustrata, origine del materiale, dimensioni reali (non l'ingrandimento!) e la collocazione (con numero di catalogo, se disponibile). Per i manoscritti in una lingua diversa dall'Inglese, è necessario aggiungere la traduzione in Inglese delle didascalie.

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Spinochitonidae fam. nov. and Spinochiton gen. nov. (Mollusca: Polyplacophora) redefined to meet the requirements of the Article 8.5 of the ICZN

107 *Giambattista Bello*
The original descriptions of the Mediterranean taxa in the order Myopsida (Mollusca: Cephalopoda)

116 *Paolo Mietto, Ermanno Quaggiotto, Francesco Giusti & Carlo Sbrana*
Taxonomic and nomenclatural notes on the genus *Idas* (Bivalvia: Mytilidae)

126 *Boris I. Sirenko & Enrico Schwabe*
An abyssal-ultraabyssal chiton (Mollusca: Polyplacophora) with a wide distribution

136 *Francesco Giusti & Pasquale Micali*
Emarginula lorenzoi n. sp. from the Tuscan Archipelago (Gastropoda: Fissurellidae)

140 *Bruno Amati & Marco Oliverio*
First record of *Acanthochitona pilosa* Schmidt-Petersen, Schwabe & Haszprunar, 2015 (Mollusca: Polyplacophora) in Spain and Algeria

145 *Jeannine Rampal*
Euthecosomata (Mollusca: Gastropoda: Thecosomata). A taxonomic review

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